

A SELECTION OF NOTES ON THE BROAD TRENDS OF DISPERSAL MOSTLY OF OLD WORLD AVIFAUNA.

by

Leon Croizat¹

INTRODUCTION :

In preparing four of my recent works (Croizat 1967, 1968, 1968a, 1968b) and a fifth not yet published (Croizat in prep.) I brought together and reviewed a mass of material bearing on the geographical distribution of Old World birds and form-making amongst them.

The late Herbert G. Deignan was a regular correspondent of mine and much of what follows I would have presented to him seeking his advice. Deignan had an outstanding knowledge of his field but to me he was particularly remarkable for his open-minded, common-sense approach to ideas new or old.

Unable now to seek his advice I wish to put on record a series of notes, which I dedicate to his memory. The notes employ a method of biogeographic analysis which Deignan supported in one of his last publications (Deignan 1963 a.) For convenience each note is given a sub-heading.

A. ON THE DISPERSAL OF *OTUS* AND *CORVUS*.

Readers will no doubt be familiar with revisions of *Otus scops* (Delacour 1941) and *Otus bakkamoena* (Deignan 1950). They may also know that *Otus scops* of Delacour is retained as two species *O. scops* and *O. sunia* by the Russians (Dement'ev and Gladkov 1951).

The distribution of these three "species" is as follows :

- *Otus sunia* extends from the Deccan to Amurland and Japan not extending south or east of a line from Ceylon-Andamans-Malaya-Labuan-Central Philippines.

1) Address: Apdo. 60262/4262 Este, Caracas, Venezuela. N.B.: Substantial alterations in style have been made by the Editor with the author's permission.

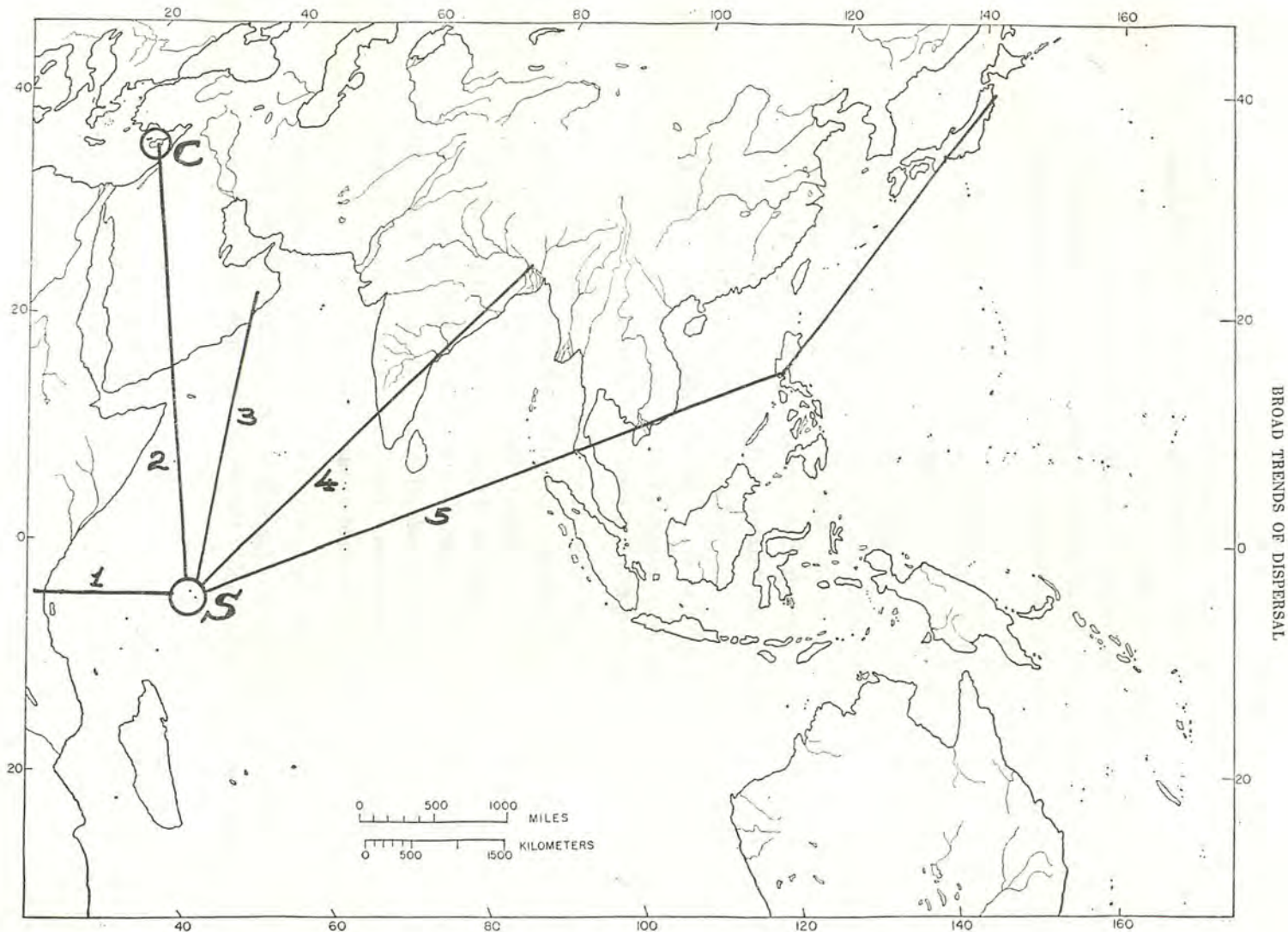
- *Otus bakkamoena* has a similar range but extends to western Arabia and western Malaysia as well (see Dement'ev & Gladkov 1951. p.369-map 59).
- *Otus scops*—omitting the forms placed with *O. sunia*—covers most of Africa, including the island of Annobón in the Gulf of Guinea (race *feae*) and Socotra (*socotranus*), Europe and Asia : Iran to the Altai; and, after what seems a broad gap, reoccurs in western North America, from British Columbia south to Mexico and within the United States to western New Mexico. There is also a local race (*rarus*) in the highlands of Guatemala. The gap between the Eurasian forms and the American forms of *Otus scops* is thus from Lake Baikal to British Columbia (see Dement'ev & Gladkov 1951 p.373—map 61).

Otus bakkamoena is universally accepted as distinct and is largely sympatric with the Indo-oriental forms of *scops* or *sunia*. These two "species" break down into four main groups of races :

- 1) African : centering around *senegalensis*, from the Cape to Sudan and Socotra.
- 2) Western Eurasian : the *scops* aggregate from Portugal and western North Africa through Europe and the Mediterranean to the Caucasus, the Near East and western and central Asia passing north of central Iran to the Altai and the approaches to Lake Baikal.
- 3) Indo-oriental : the *sunia* group.
- 4) American.

This is a vast and rather controversial assemblage and I cannot pretend to judge it as an ornithologist; however, to the biogeographer it poses a single direct question, "where is the hub of its dispersal ?" Does it lie in 'Holarctis' or 'Antarctis' (southern South Africa) or in the tropical zone ?

Peters (1940) remarks in a footnote on p.97 that *Otus insularis* (island of Mahé in the Seychelles) "possesses no characters that entitle it to recognition as the monotypic genus *Gymnosops*. Stresemann 1925 p. 195, note, believes it to be related to the *scops* group; in my opinion it is a *bakkamoena* offshoot."



Map 1. To show the links between the Seychelles (*S*) inhabited by "*Otus insularis*" and the mainland populations of *O. scops-senegalensis* group (1); *O. scops*, nominate group (2) and various populations of *Otus bakkamoena* (3, 4 and 5). C. marks Cyprus. See text p. 258.

Since this endemic form shows links with each of these species the Seychelles pinpoint the divide between *O. scops* and *O. bakkamoena*. Let us then set down (Map 1) a node from which run "tracks" in different directions—Africa, the Mediterranean and Europe, Arabia, Indo-malaya northward to Japan. Remember too that within this net of dispersal and affinities the question of the affinity of the Seychelles owl is still unsettled.

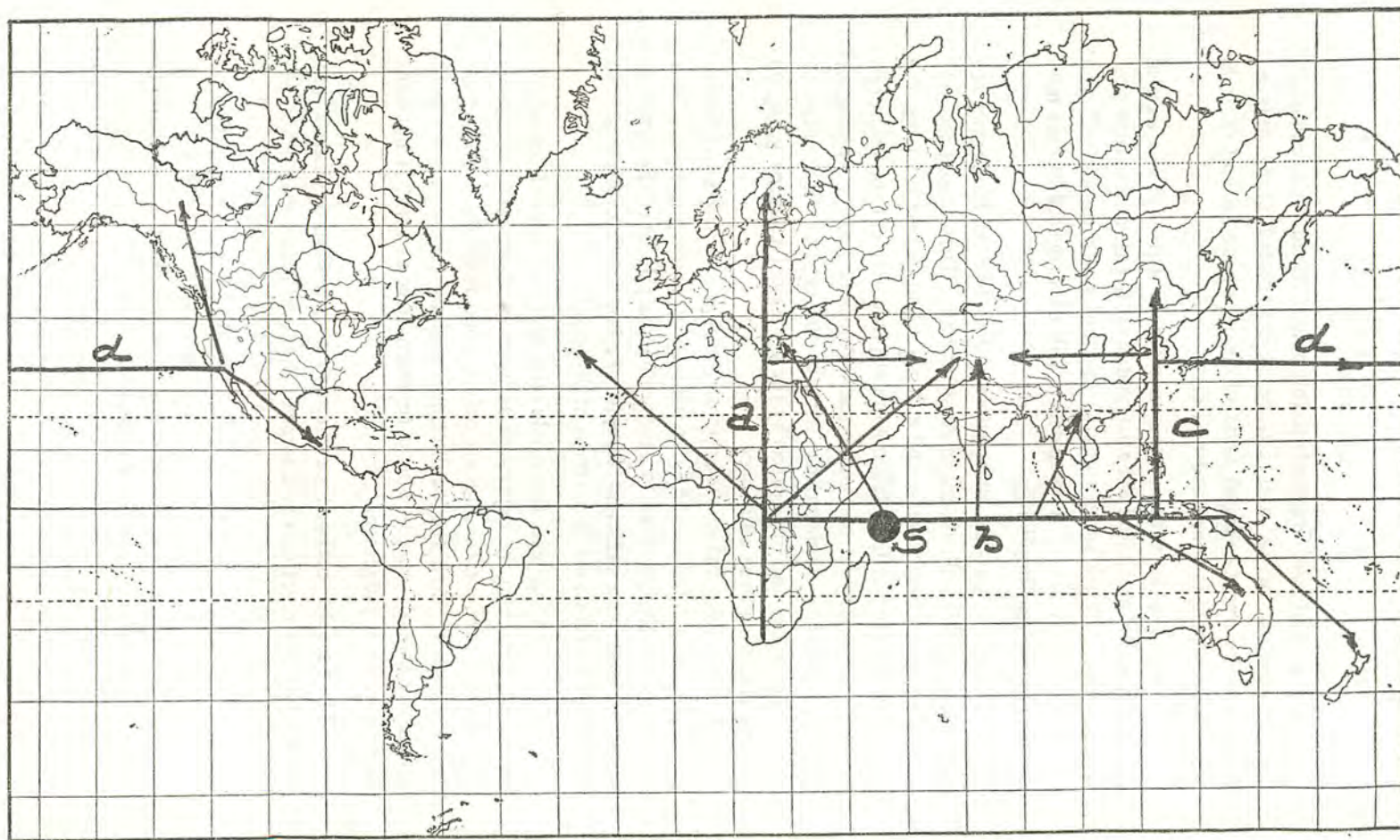
Regardless of how the question is settled the Seychelles do form a node of dispersal¹ with far-flung connections.

The significance, value and purpose of the term biogeographic—"track" has been amply covered in previous works (Croizat 1958, 1962) it is by no means a conventional 'line of migration', rather it is, briefly, a symbolic line intended to make clear at a glance a trend of dispersal. Although approximate in the sense that it can be replaced with more detailed outlines and symbols whenever the range of a particular taxon needs to be, or can be, shown in complex detail, a "track" is by no means imaginary—it always runs basically true to actual records and, properly analysed, yields their data.

For example one might suppose that the "tracks" in Map 1. that radiate from the Seychelles are too loose to be meaningful. Take however the "track" to Cyprus: Delacour (1941) discussed the endemic race *Otus scops cyprius* in these terms: "Markings very distinct and rather strongly resembling those of the gray phase of *Otus scops sunia* and *Otus scops senegalensis*" clearly stressing the links with Asian and African populations. Both this and the remarks by Peters about *Otus insularis* are reflected by the "tracks" in Map 1.

At this point let us introduce for comparison certain main axes of dispersal (see Map 2). Looking at these you may suppose them imaginary, or, at best, highly theoretical, but open your mind and suspend your judgement awhile.

1) General statements and terms are by implication referring to my previous works, and to their indices. For example the status of the Seychelles in biogeography can be traced easily from the index to "Panbiogeography" (Croizat 1958).



Map 2. To show the main axes of dispersal (a,b,c, and d.). Unmarked arrows represent connections of a secondary character. S. marks the Seychelles and is given to help relate the "tracks" shown in map 1. to the main axes.

Let us relate the *Otus* owls to this map. Broadly you can grasp that *O. scops* in Africa and Europe is distributed along axis **a.**, *O. bakkamoena* and *O. (scops) sunia* along axes **b.** and **c.** and *O. scops* in the New World is connected by axis **d.**

In initial explanation of this map suffice it to say that axes **a.** and **c.** run south-north and axes **b.** and **d.** west to east and east to west respectively. "Why south to north and not north to south?" you might pertinently ask. This question will be answered by this note both explicitly and implicitly.

Consider in passing that whole orders like the Piciformes are distributed world-wide except in Australasia. These could scarcely have dispersed along axes **a.** and **c.** if they had "come in" from the central or western Pacific. It is not out of place to refer to other orders. It would seem illogical to assume that evolution, and its by-product dispersal, proceed haphazardly without the constant influences of time and of space and unaffected by the geological changes going on through the same time and space.

Far more logical is it to suppose that life as a whole has indeed been linked or related by the same palaeogeographic processes. This hypothesis can be subjected to a searching analysis since the accumulation of data on a sufficient sample of plants and animals should yield clear correlations in patterns of dispersal.

This then suggests the whole—the body of data—from which the conclusions may be expressed as "axes of dispersal". Opinions on dispersal differ and theories are only as good as the data upon which they are based. Are the conflicting opinions that you may hold sufficiently broadly based to be as representative as this? If not continue to suspend judgement.

The "tracks" mapped for *Otus* pay no attention to climate, but climate has had its effects and some of the local forms may be closely related to climatological or ecological factors. The catholic distribution of *Otus* as a whole suggests that broad dispersal as such preceded adaptation of the various forms to such local factors. This catholic distribution is seen in the Strigiformes quite commonly—for example in *Tyto*, *Bubo*, *Glaucidium*, *Strix* and *Asio*.

Let us look now at the detailed situation in India for *Otus scops* including *sunia*. According to Ripley (1961) 4 races occur :

- 1) *pulchellus* : a winter straggler south to the Sind and Baluchistan.
- 2) *sunia* : from Burma along the Himalayas to Garhwal—to the west of Nepal—and southward.
- 3) *rufipennis* : in the Deccan, from Kerala northward.
- 4) *leggei* : in Ceylon.

Of these *pulchellus* belongs to the *scops* group. It breeds from about the longitude of Moscow east to the Altai in Central Asia and migrates south, reaching as far as Sind, Baluchistan and the Nile valley. Its area of occurrence in India matches well birds, whether migrant or resident, which according to Meinertzhagen (1928) are authentically "palearctic".

The three remaining forms belong to the *sunia* group.

With reference once more to the axes of dispersal in map 2. *pulchellus* occurs from the direction of western axis a.; *leggei* and *rufipennis* from southern axis b. and *sunia* from the direction of eastern axis c.

On this basis it seems indeed possible that an area including the Himalayan chain has been "invaded" from the south, the north-west and the east (see Swan 1961). In respect of east and west it should be remarked that a boundary of some significance has been statistically demonstrated to lie roughly between eastern Nepal and western Bhutan. It is useful to have this in mind when considering the tangled skeins of biology in India.

In the case of *Otus scops* and *Otus sunia* it is not unreasonable to suggest that the complex is bicentric in Eurasia—the different parts appearing at opposite ends of the Himalayan chain.

Furthermore it seems possible that as regards India in general some of its bios may have their origin from the south, from points along axis b. This theory, as it should be regarded at this point by

the reader unfamiliar with my main works, leads to practical conclusions which can be drawn and which will be developed throughout this article.

In summary using a system of plotting "tracks" on a map—in this instance for *Otus* species—we have introduced a framework of thought to assist in the consideration of problems related to evolution and dispersal over space through time.

The particular points made—the axes of dispersal—are no longer wholly hypothetical: statistical verification is implicit from my major works (Croizat 1952, 1958, 1960, 1962, 1968, 1968a). If the reader accepts this statistical verification and applies the broad methodology proposed to verify the evidence on dispersal, he must be prepared to free his mind of other unsubstantiated theories many of which have become part of the "accepted" doctrine of biogeography and related sciences.¹

This article will, hopefully, demonstrate the methodology at work.

The taxonomy of the genus *Corvus* has been revised by Meinertzhagen (1926), Amadon (1944) and Dorst (1947). Subsequently it has been reconsidered and listed in Peters' Checklist Vol. XV (1962) by Blake & Vaurie.

The reviewers are not always in agreement, but by cross-referencing their views one can establish for example that Meinertzhagen, Amadon and Dorst all accept a certain affinity between *Corvus albus*, *C. corone* and *C. torquatus*.

Let us examine the distribution of these birds:

1. *C. albus* (monotypic): Africa, north of Cape Province to a line from Senegal to Ethiopia, and the outlying islands (Fernando Po, Madagascar, Comoros, Assumption, Aldabra, Zanzibar and Pemba).

1) See Croizat 1962 page 595, in which I have mentioned the criticism of Stanley A. Cain (Torreya 43: 132. 1943) of the "burden of hypothesis and assumptions" carried by the "sciences of geobotany and geozoology," and in which I have gone on to suggest a constructive approach to the problems thus created.

2. *C. corone*:

C. c. orientalis: from Iran, the Pamirs and Tianshan east and north to Kamchatka, the Kuriles, Sakhalin—bounded on the south by western Tibet, southeast Yunnan and northern Indochina, and west and north to southeast Transcaspia.

C. c. corone: the western part of Europe from the Iberian Peninsula to western Czechoslovakia and the river Elbe and north to Scotland.

C. c. cornix: eastern Europe, east of the range of the previous race and as far east as the Urals and south to the Crimea and the Danube basin. Reoccurring in Scotland and adjacent islands, Ireland and, at least on passage and in winter, on the Atlantic coast of France (Dorst 1962).

C. c. capellanus: from Iraq to SW Iran.

C. c. sardonius: Egypt (north of Aswan), Asia minor, the Balkans (north to the Danube), southern Italy and the Mediterranean islands (Cyprus, Crete, Sicily, Sardinia, Corsica).

C. c. sharpii: Iran (from the Zagros Mts. to Khorasan) north through the Caucasus to western Siberia, east to the Yenesei.

3. *C. torquatus* (monotypic): western and south-western China, north Indochina (Tonkin and N. Annam), Hainan and possibly Manchuria. Reported from Taiwan as straggler but not from Thailand (Deignan 1963).

This looks complicated but one can readily observe that *C. albus* meets *C. corone* between the Sudan and Egypt and that *C. torquatus* meets *C. corone* in the region of the highlands of S. China and northern Indochina. Map the "tracks" and you will see that by and large they accord with axis a. in map 2.

It is well worth stressing that the biogeography of this group of crows is not changed by differing taxonomic opinions. Hence the treatment of *albus* as a race of *C. corone* by Meinertzhagen (1951) would if followed alter the former classification but it would not change the affinity nor the locality record.

Taxonomy is the formal naming of a group or taxon for the purpose of classification and is thus quite distinct from taxogeny which inquires into the causes or origins of a taxon with particular attention to matters of time and space.

In my view the competent taxonomist should find these two inseparable since he should have causes (established through taxogeny) for what he classifies (by taxonomy).

Amadon (op. cit. supra p. 16) suggests that "*albus*... may be an African representative of one of the Asiatic groups and perhaps should come near *torquatus*". The competent biogeographer readily accepts the first phrase and examining the second, looks past its geographical improbability because of the wide gap in the ranges of these two birds and finds it taxogenetically entirely feasible. It is a well known fact that the populations occupying the centre of the range of a taxon may differ markedly from one another whilst the populations at diametrically opposite points on the periphery of the range of the taxon may be remarkably similar. I have dealt with "wing dispersal" elsewhere (for example Croizat 1962).¹ *Corvus albus* and *C. torquatus* exhibit

- 1) The manifestations and causes of "wing dispersal" really require a full paper but let us digress onto one example. The piculets, genus *Picumnus*, 'mass' in the New World, particularly in Brazil, but "send" a species *innominatus* to Indo-Malaya (Croizat 1962, 1968). There is no likelihood or question of the Indo-Malayan *P. innominatus* having arrived from Brazil after a voyage "in the eye of a storm". Its existence at the eastern "wing" of piculet distribution is the result of the pool of ancestral genes recombining with closely similar results in the New World and Indo-Malaya, and with less similar results in Tropical Africa, genus *Verreauxia*, and in Indo-Malaya again with the genus *Sasia*. These examples of form-making and distribution are often so spectacular that "zoogeographers" and "phytogeographers" avoid them (see also Croizat 1952, p. 12; 1960, vol. 1b, p. 1486; and 1962, p. 21 et seq.). In fact of course explanation is no harder than in the case of differentiation between birds 100 miles apart. The genetic pool constantly recombines characters. It does so most actively where the opportunities are greatest and the characters more numerous. By contrast on the "wings" the shuffling is less easy. Hence the overuse of "relictual forms" and the often discovered "puzzling similarities". There is a clear parallel in the points of survival of the archaic forms of a language.

"wing dispersal" in relation to the middle ground occupied by *C. corone* and it is significant that the latter is polytypic whereas *albus* and *torquatus* are monotypic. This alone suggests that Amadon's concept of a complex involving *corone*, *albus* and *torquatus*, in which the latter two are most alike despite their ranges, is highly probable.¹

Amadon (op. cit. supra p. 15) also suggests that *Corvus tristis*, which is monotypic in New Guinea stands somewhat apart from its allies by reason of partial loss of the head feathers and its dull coloration and here I must beg to digress substantially.

Meinertzhagen (1926) considered this crow the oldest form in the genus *Corvus*. In New Guinea also is found "the most primitive" Dicrurid (Vaurie 1949, p. 210 et. seq.). This bird *Chaetorhynchus papuensis* is monotypic and the sole representative of this genus. Also in New Guinea the birds of paradise are considered "odd" crows. All of this is "wing dispersal". That forms of life which have largely or completely disappeared from other continents survive only in Australasia and the New World (e.g. *Mesomyodes* among birds, Marsupials among mammals etc.) strongly suggests that Africa and its approaches are indeed the ultimate hub of dispersal of "modern" higher life.

It was once observed (for original quotation and comment see Croizat 1958, Vol. 1, p. 218 footnote) that none of the families which are clearly South American in origin has developed species that have crossed into the Old World. In my opinion the explanation is that South America, like Australia has always been at the receiving end, and that S. America and Australia each developed within their limits, and often to a massive pitch of secondary radiation, taxons of which

1) Dr. J.T. Wiebes of the Rijksmuseum, Leiden has just sent me a copy of his study (Wiebes 1968) of the genus *Goliathus* (Coleoptera: Cetoniidae) in Africa. In this "wing dispersal" is evident in the 4 species of the subgenus *Fornasinius* and the author remarks "There are more examples of this phenomenon in other groups of African Cetoniidae". This I well believe and I would add that the patterns of distribution shown by the species of *Goliathus* are matched so perfectly by birds and plants that the identities could be exchanged (Croizat 1960, 1b. p. 1451 et seq.). See also my comments (Croizat 1958, Vol. 1, pp. 592-4) on MATTHEW'S LAW.

the ancestors were originally received from another intermediate centre thus corresponding to Africa.

Africa is not here used in the precise geographic meaning of today but it is used for the chunk of the "Gondwanic Land Mass" which stood between America and Australasia during Jurassic and Early Cretaceous times, and which by subsequent fractures has become moulded into the Africa we know today. The Africa referred to is one therefore in which it would be hard to determine Ceylon from Socotra and Arabia or the Seychelles from Ceylon and Madagascar.

It is a matter of record that fossil evidence exists of plants, fishes, reptiles, mammals and birds from the same epochs (Triassic to earliest Cretaceous); this despite plants being earlier in the scale of life than fishes, fishes earlier than reptiles, and reptiles earlier than mammals and birds. This can only be explained by postulating a primordial very powerful fillip to evolution starting in pre-Triassic times and working itself up to a pitch in the ages following. It seems unavoidable to associate this with the Permo-carboniferous Ice Age since:—

1. A similar surge followed the Infra-Cambrian Glacial Eras Harland & Rudwick 1964, Croizat 1967a pp. 143 et. seq., Croizat 1968a p. 421).
2. The origins of the angiospermous plants definitely point to the southern continents—the sector of the earth visited by the Permo-Carboniferous Ice Age.

It cannot be said that Africa is the only major centre of evolution that can be detected e.g. for plants as witness the Western Pacific (Croizat 1952, 1968), but such other centres as can be detected are clearly and constantly linked with Africa and its approaches.¹ We shall have renewed evidence of this in this article.

1) Recent advances in geophysics handsomely confirm the chronology of dispersal, and certain of its fundamental features, advanced by me nearly 20 years ago (Croizat 1952). I then remarked the presence of major nodes of angiospermous dispersal, for example in the area adjacent to eastern Africa and in the west-central to south-western Pacific—the "gates of angiospermy". One of my reviewers was sufficiently perturbed to enquire whether I was a genius or a crackpot and obviously the latter seemed more probable to him! Now geophysicists—who unfortunately do not often know of my works—have come to the conclusion that two "poles of spreading" of the ocean floor are located, one in "north Africa" and the other in the Pacific "north of New Zealand" (Heirtzler 1968). The coincidence between these "poles" and the "gates" that I suggested deserves deep consideration.

Looking again at *Corvus* we find that **Amadon** (1944) thinks that: "*C. splendens* and *frugilegus* suggest one another in some respects, but this may be parallelism". Unfortunately the term 'parallelism' has become so much of a catchword that it has virtually lost concrete meaning. To evaluate its meaning in this particular case, let us examine the distribution of these two crows:

– *C. splendens* (not split by race): Western Arabia (Muscat), "introduced to" Zanzibar¹, Maldives and Laccadives, Ceylon, Baluchistan, India, Burma south to Tenasserim and the northern peninsular provinces (Petchburi and Prachuap Khiri Khan) of Thailand.

– *C. frugilegus*:

C.f. frugilegus: from Iraq and Iran north and east to the Tianshans and Mongolia, in Siberia east to Yenisei: north and west to the Caucasus, northern and western Europe south to France and Spain (an isolated colony in León).

C.f. pastinator: from the Altai to Yakutia, Manchuria, Korea and north and northwest China (eastern Sikiang, Szechuan).

The geographical hinge between these two species is a short one between Arabia and Iraq. There is no reason why *C. frugilegus* should not extend widely south of Iraq as it does north of there—no reason of climate or ecology that is. It is remarkable how narrow is the area of contact between these species. Relevant to this are my discussions of *Prunella* and of *Pyrrhocorax* (**Croizat** 1958). From the same point then, *C. splendens* "streams" eastward whilst *C. frugilegus* moves northward spreading out both to east and west. The pattern is similar, though less extended to the East, to the pattern shown by the group of owls examined above.

1) **Meinertzhagen** (1954) records this crow from Aden and Port Sudan in the Red Sea. A bird taken in Aden is reported to resemble the Ceylonese race *C.s. prolegatus*, whilst birds from Muscat belong to the race *C.s. zugmeyer* of the Sind and Baluchistan. **Meinertzhagen** quotes the report of **Malcolm Davis** (Auk 1951 p. 529) of some of these crows, which had been blown aboard his ship off Ceylon, flying ashore in Somaliland (Cape Guardafui). From these reports one would expect *C. splendens* to be better established in its outposts than seems to be the case.

'Parallelism' can in this case then be defined more clearly. Here are two offshoots—parallel offshoots if you will—of an original ancestor which developed a split between Arabia and Iraq. Note that the hinge reaches down to the Maldives and Laccadives showing a similar pattern again to the owls, in which the Seychelles form the extension of the hinge. The evidence suggests an important hinge of dispersal with its axis on the islands of the Indian Ocean.

Amadon (op. cit. p. 15) is satisfied that within *Corvus* a natural subgroup comprises the first ten species he lists: *tristis*, *fuscicapillus*, *validus*, *unicolor*, *typicus*, *moneduloides*, *woodfordi*, *meeki*, *kubaryi* and *enca*. In Peters's Checklist *meeki* is treated as a race of *woodfordi*, and *unicolor* as a race of *enca*; examining the distribution of the eight species that emerge we find:

1. *C. enca* (7): Malaya, Riouw Archipelago¹, Sumatra (including the islands of Nias, Simalur and the Mentaweis), Borneo, Celebes, Buton, islands east of the Celebes (Banggai, Mangoli, Taliabu, Sanana), Moluccas (Ceram and probably Buru), Philippines (Mindanao to Samar, Palawan).
2. *C. typicus* (1): Celebes, Buton.
3. *C. validus* (1): Moluccas
4. *C. fuscicapillus* (2): Arus, Western Papuan Islands, NW New Guinea.
5. *C. tristis* (1): New Guinea and adjacent islands (Japen, Entrecasteaux etc.).
6. *C. woodfordi* (2): Solomon Islands
7. *C. moneduloides* (1): New Caledonia
8. *C. kubaryi* (1): Marianas

Five of the eight are monotypic; the brackets above contain the number of races of each as per the Checklist. Baker (1951) treats *C. florensis* as a race of *C. enca*, following Amadon (op. cit.) and Peters and believes that *kubaryi* is closer to *enca* than to *macrorhynchus*.

1) I have already remarked upon the significance of this group of small islands lying just south of Singapore (Croizat 1968).

This pattern quickly strikes the biogeographer as but one of the many patterns of distribution which starting from the region of Malaya and the Greater Sundas "streams" eastward to western Polynesia, stopping at the front Marianas-New Caledonia (Croizat, in partic. 1968, p. 238 fig. 29 and p. 292, fig. 38).

Not being an ornithologist I cannot hazard a guess as to the affinities of *C. enca* west of Malaya and the Greater Sundas and with the limited means at my disposal I can find no published ornithological opinion on this. Perhaps, like the pigeon *Caloenas*, it stands "isolated." This, of course, simply means that it is the issue of some ancient stock to which it is difficult to trace it back. Considering the trends of overall dispersal however it would seem indicated to look for the ancient stock in question in the direction of Africa—to the west of Malaya and of India. The dispersal of the group does in fact follow a track along the line of axis *b*. in map 2., although it "skips" the Lesser Sundas.¹

As mentioned above, Baker accepts a relationship between *kubaryi* and *macrorhynchos* though a more distant one than between *enca* and *kubaryi*. Amadon (op. cit. p. 16) goes no further than sub-groups and he places *macrorhynchos* in a group of eight species 'most of' which are 'probably allied', and follows the group with *C. albus* saying "which may be an African representative of one of the Asiatic groups...". Of the eight *corone* and *torquatus* have been listed above, the others work out as follows:

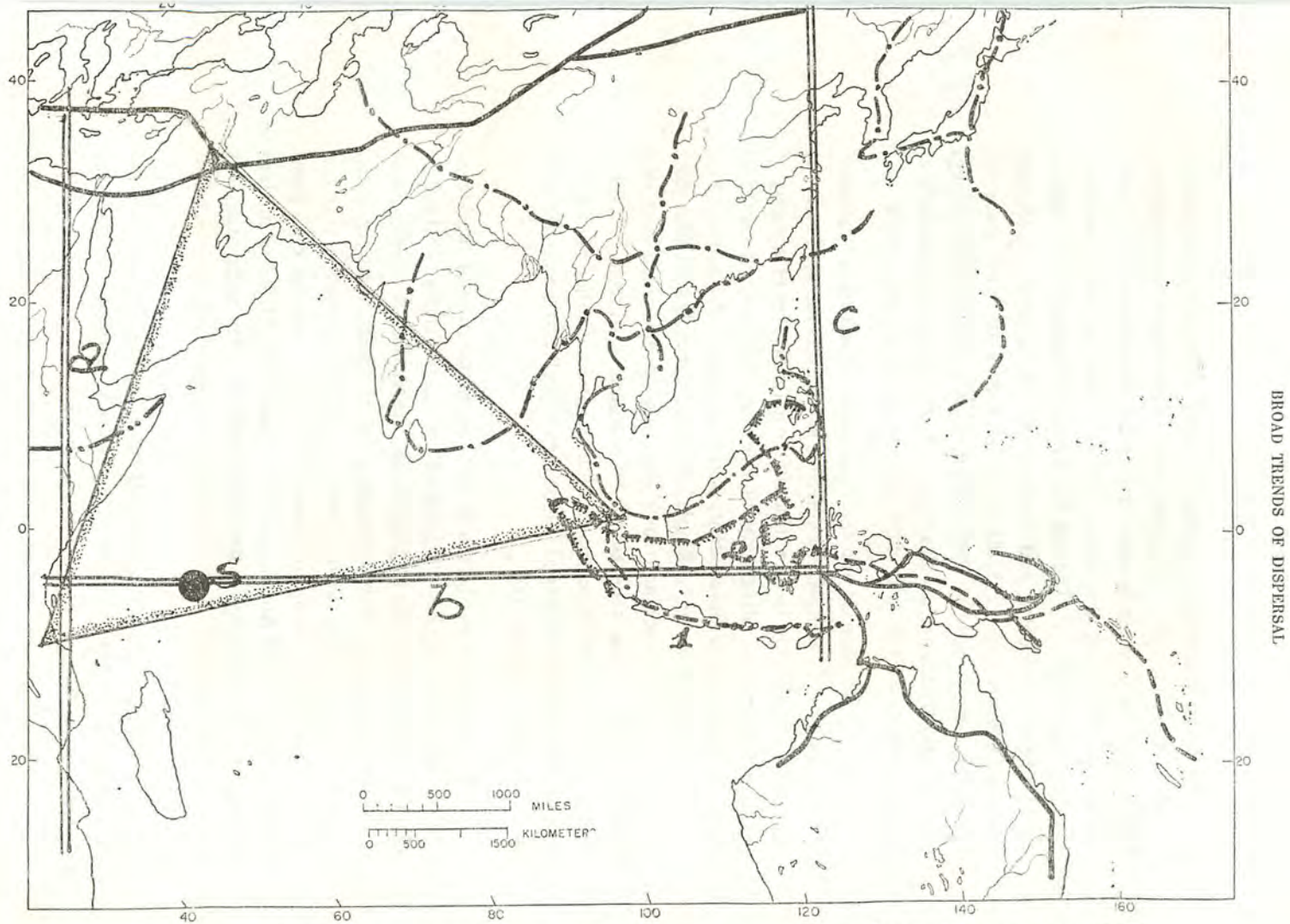
- *C. corax*: Iraq and Iran, fanning out to the whole of colder Eurasia and North America and including the Mediterranean—from coastal Egypt, Crete and Greece to Morocco and the Canaries. If Dement'ev & Gladkov (1951) are right in placing *ruficollis* as a race of *corax* then the range of the species stretches south to a front: Cape Verde, Nigeria, Somaliland.

1) 'Skipping' the Lesser Sundas is a feature of the dispersal of a great many plants which is commonly attributed to such factors as the existence of a monsoon climate on these islands or the sea to their north being 'muddy' (see Van Ooststroom on *Ipomoea maxima* in Van Steenis (1948-54), Vol. 4., p. 475). This facile explanation may be valid in some cases but too many other fundamental aspects of Indonesian dispersal suggest otherwise (Croizat 1958, 2b.: 863, fig. 240 and 894, fig. 246 a.).

- *C. macrorhynchos*: Ceylon, India and the Andamans south through Indo-China, Thailand and Malaya and Malaysia to the easternmost islands in the Lesser Sunda Chain (Timor and Wetar) and east to Taiwan, Hainan, China, the Riukius, Japan, Korea, the Kuriles, Sakhalin, Amurland and the Bonin Islands.
- *C. orru*: the Moluccas, New Guinea and adjacent islands—New Britain, the Louisiades etc.
- *C. coronoides*: Australia and Tasmania.
- *C. bennetti*: Western and South Australia to the Gulf of Carpentaria and W. Queensland.
- *C. cryptoleucos*: Western United States and Mexico (Nebraska, Colorado, New Mexico, Arizona to Tamaulipas and Guanajuato).

On this grouping let me make the following points:

1. If *kubaryi* is related to both *enca* and *macrorhynchos* and the latter species is involved with *corone* and *torquatus* it follows that *enca* itself has common ancestry with *corone* and *torquatus* in some archetypic "crow of the Indian Ocean".
2. The group envisaged by Amadon "departs" from Africa for the North and eventually the New World, basically along axis a. in map 2. East of Ceylon it also follows axis b., veering northward out of Malaysia along axis c. to reach the Kuriles, finally crossing to the New World along axis d. Mingling with the *enca* aggregate a front is established in the Pacific: Bonins—Marianas—New Guinea. South of New Guinea run two "beams" (see Croizat 1968: 36, fig. 5. and Croizat 1962: 154, fig. 39b.) from New Guinea to Australia and Tasmania and from New Guinea to New Caledonia. Map 3. shows these trends of dispersal schematically and mirrors features standard with bird or plant distribution as seen by the biogeographer.



KEY : — *Corvus corax*; *C. ruficollis*; - - - *C. enca*; - · - eastern allies of *C. enca* (see text);
 - - - *C. macrorhynchos*; ——— Australasian allies of *C. macrorhynchos* (see text).

Map 3. To show the "tracks" of *Corvus*. The triangle with the stippled border incorporates an element of each group. Note that *C. macrorhynchos* occurs through the Lesser Sundas (1) whilst *C. enca*, and its allies, does not (2). The symbols a, b, c, and S. are repeated from map 2.

One can commence plotting "tracks" from the ocean and its islands to the south of Arabia and India or one can commence from Malaya and the Greater Sundas; the pattern is constant and it insists, by its repetition, on the same "tracks" and the same ancestral "cradles" or "nodes". The hub lies within a triangle with its apexes on Madagascar, Socotra and Ceylon on the adjacent mainlands. Pigeons (Croizat 1968: 238, fig. 29), and crows and owls trace the same story: different taxa, different affinities and different groupings but the main trends are always there. If my reader still doubts this he is urged to verify it with plants or animals of his own choice.

During the Jurassic and the Triassic the ancestors of "modern" life spurred by the Permo-Carboniferous glaciations radiated to cover the earth. By the mid to late Jurassic the main centres of massing or conglomeration, and ultimately of form-making, were established virtually where their descendants still live today. A 'modern' bird may only go back to, for example, Miocene times but its ancestors within a steadily branching tree of life are older and reach back into Jurassic times. It is unnecessary to postulate a flittering, restless dispersal throughout these times which answers neither rhyme nor reason: its 'modern' dispersal can be seen as a clue to the distribution of its ancestors step by step.

To those who would claim that the distribution of the Megapodidae belies this as they "originated" in Austro-malaya and subsequently "emigrated" to the Philippines and the Nicobars—points outside their "ancestral range" I would suggest that the megapodes represent, as do the Cracidae, an earlier level of galliform evolution that has survived only in the wings of an arc of dispersal centred on a point between America and Australasia—hence again, the 'Africa' of modern geography. The marsupials are a parallel case. The same argument holds for the survival, and massive development, of mesomyodian bird life in the New World. The point is simple but like all simple points it is lacking in conviction without a massive, painstaking and hard-to-read elaboration of the botanical and zoological evidence, for which the reader must see all my other works.

If dispersal had indeed been footloose then patterns would not be repetitive and marked differences in a fauna or flora—as for example the differences between east and west in the flora of Colombia and Venezuela—would not be so evident as they are. **Sclater** has already insisted on this point (**Wendt** 1967) in commenting on the “migrationist” theories of **Darwin**’s followers (**Croizat** 1962).

Were I to be asked whether thirty years of research into dispersal has been rewarded by the finding that dispersal is orderly and logical and thus capable of statistical analysis and synthesis I should answer categorically “Yes”. Furthermore, it would seem that **Deignan** (1963 a.) came to the same conclusion.

B. ON THE MASSING AND DISPERSAL OF FRINGILLIDAE, ESTRILDIDAE AND PLOCEIDAE.

Paynter (1968) states in the Introduction to Vol. XIV. of **Peters**’s Checklist that the three families which I now propose to subject to biogeographical analysis are among the best known and goes on to say “in spite of the abundance of taxonomically useful information, or *more probably because of it*, the systematics of these birds are among the most unsettled and controversial in the class Aves” (italics mine).

I do not see why taxonomic information should be self-defeating even if it should lead for example to the conclusion that *Serinus estherae*, *Pholidornis* or even *Fringilla* species are difficult to place in the system. Formal taxonomy, whether it deal with botany or zoology, rests essentially upon definitions and keys and because it is often

impossible to draw these up in a watertight fashion it has definite limitations.¹

-
- 1) To give but one example : try to delineate the differences of the Turdinae from the Timaliinae, and take a special look at *Cataponera*—endemic to the mountains of, of all places, the Celebes—a “thrush”, and *Garrulax* which is well distributed in the highlands of Indo-Malaya—a “babbler”. A competent biogeographical analysis of these two sub-families would show that they ‘mass’ differently : though the differences are smaller than those between, for example, the Fringillidae and the Estrildidae.

The Timaliinae are indeed the “thrushes” of the tropical Far East and western Malaysia. The problem which the dispersal—in this context, the distribution and form-making—of the Timaliinae poses the able student begins with the following figures :

1. The sub-family includes 44 genera of which only one, *Chamaea*, is American (and contains one species with six races).
2. Africa has representatives of only 8 genera (ca. 18%) of which 3 : *Turdoides*, *Trichastoma* and *Alcippe* : are large genera shared with Indomalaya, 1 : *Neomyxis* with 4 species and a total of 10 races : is confined to Madagascar, and 4 : *Ptyrticus*, *Lioptilus*, *Parophasma* and *Phyllanthus* : are small, purely African genera. Of 102 races listed from Africa 51 belong to *Turdoides*, 22 to *Trichastoma* and 7 to *Alcippe*. The remaining genera can gather only 22 races between them.
3. Peters's Checklist puts Assam within the distribution of 117 different races... 15 more than for the whole of Africa !
4. Thailand counts 22 genera (50% of the total in the sub-family), 68 species and 133 races (Deignan 1963)! In reaching this sum Thailand benefits from its position between 3 different centres of evolution :
 - in the north : Nepal to Assam and Burma.
 - in the east : Indochina, indicated by the plateaus of Langbian and Bolovens (which between them yield 23 races of babblers, mostly endemic).
 - in the south : Malaya and the Greater Sundas (Malaya counts 44 races of babbler as does Borneo whilst Sumatra has 41 and Java 25) with interesting but disconnected links with Indochina, as for example in *Crocias*. The influences from the north and south meet in the region of Prachuap Khiri Khan (Thailand)/Tenasserim (Burma) and the Isthmus of Kra (Croizat 1958).

These figures are meaningful and as they are not theoretical their consideration will earn dividends and not lead to the universal panacea of “chance” or “casual means”. This footnote however is not the place to examine them further.

Although formal taxonomy is thus limited it can, with the addition of notes or footnotes of clarification, make its intent clear.

I propose to omit the genus *Fringilla* as my good friend Michel Desfayes is working on this; so let us commence the Fringillidae with the sub-family Carduelinae, thus finding 19 genera. These ranked by numbers of species are as follows :

<i>Serinus</i>	33
<i>Carduelis</i>	24
<i>Carpodacus</i>	21
<i>Coccothraustes</i>	9
<i>Pyrrhula</i>	6
<i>Acanthis</i>	6
<i>Rhodopechys</i>	4
<i>Leucosticte</i>	3
<i>Loxia</i>	3
<i>Pinicola</i>	2

plus the monotypic genera : *Linurgus*, *Rhynchostrutius*, *Uragus*, *Nesospiza*, *Chaunoproctos* (extinct), *Callacanthus*, *Urocynchramus*, *Haematospiza*, *Pyrroplectes*. Of these monotypic genera the first three are not truly monotypic as there are racial variations. It is also interesting to note that the last four genera named all hail from the Himalayas or their immediate approaches.

Analysis of the distribution data in the Checklist may easily be made by the reader and I will dispense with the listing of details. The genus *Serinus* appears clearly to be massively African : about 26 out of 33 species or some 79% of the genus. None of the species is listed for Madagascar but some reach Arabia and there are a few records from islands in the Gulf of Guinea. The remaining seven species are in Europe, 2; Arabia to Asia-mainly temperate zone, 4; and the last species *estherae* follows an unusual distribution pattern of its own : shown by races this is as follows :

<i>S. e. vanderbiltii</i>	:	N. Sumatra	--	montane
<i>S. e. estherae</i>	:	W. Java	--	montane

- S. e. orientalis* : E. Java — montane: Tengger Mts.
above 2000 m.
S. e. mindanensis : Mindanao — montane

From the taxonomists' standpoint this distribution does not fit too well into the general pattern of the genus, and I shall return to this point later.

In contrast with *Serinus* the genus *Carduelis* totally lacks representation in Africa, counts 2 species in Europe and 5 in temperate Asia whilst in America there are 19 species: again about 79% of the genus.

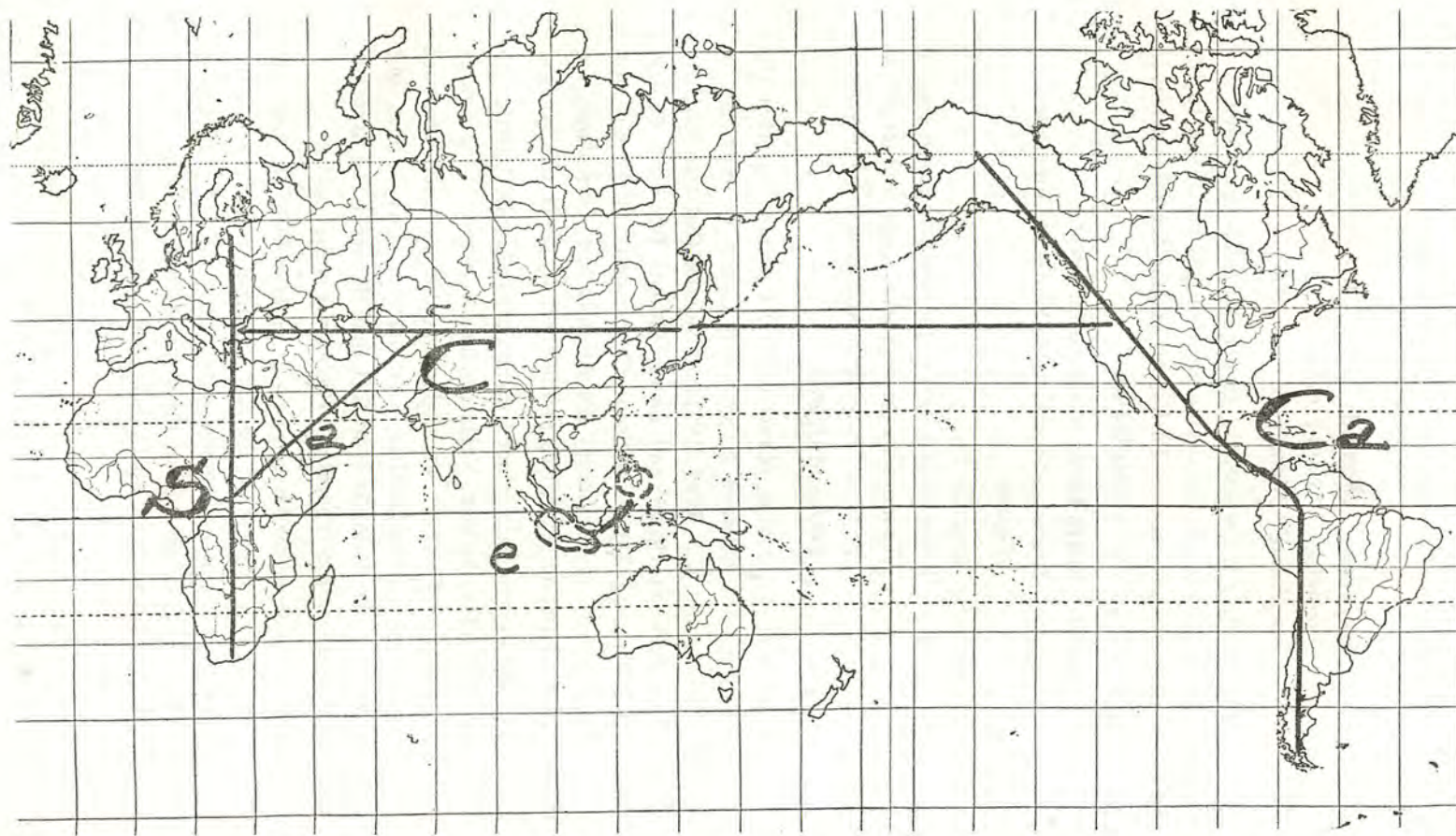
Carpodacus also has its place: Asia lists 18 species, one of which is shared with Europe, leaving three in America. The Asian share is thus about 85%.

These percentages which characterize these three largest genera indicate that there are three centres and the details suggest that the Carduelinae "departed" from the Cape and, leaving the bulk of *Serinus* in Africa, moved into central Asia "unloading" the bulk of *Carpodacus* in the vicinity of the Himalayas, and passing east towards the Pacific "invaded" the New World, delivering to it the main stock of *Carduelis*. This is shown diagrammatically in map 4. and it corresponds closely with what I have earlier called *genorheitron* (Croizat 1952).

This track is in fact one of the oldest on record for the Eocene and it is reasonable to assume that ancestral types of these "modern" passerines existed long before the Eocene preserved their descendants, and that they were already deployed along an arc which would take in Capetown, Irkutsk and Mexico City of today. It is also reasonable to suppose that from this ancestral stock arose, step by step, but without much change in the areas of massing, the "modern" genera and their species.

No feature of biogeography causes *Serinus*, *Carduelis* or *Carpodacus* to be difficult to resolve in taxonomy.

I do not propose to deal with the affinities of the Estrildidae. Whether they are closer to the Fringillidae or to the Ploceidae is a matter for my ornithological friends to decide. Let us however look at their dispersal. The Checklist lists the following subfamilies (shown with their number of genera):



Map 4. To show the "tracks" of the Fringillidae. The letters draw attention to the main massings of *Serinus* (S), *Carpodacus* (C) and *Carduelis* (Ca). The diagonal track (a) indicates a direct link from Africa to Central Asia and the Himalayas. The range of *Serinus estherae* (e) is also depicted. See text pp. 275-6.

Estrildae	Waxbills	16
Poephilae	Grass Finches	5
Lonchurae	Mannikins	6

and in addition there is the interesting genus *Pholidornis* which is a frightful conundrum to the classifying ornithologist but a gem to the biogeographer or taxogenist. *Pholidornis rushiae* the sole species in the genus has the following distribution:

- P. r. ussheri* Sierra Leone to Ghana, in forest.
- P. r. rushiae* Southern Nigeria to the Southern Cameroons and Gabon
- P. r. bedfordi* Fernando Po
- P. r. denti* From Yokadouma in the extreme south-eastern Cameroons through central and southern Congo to north-western Angola and to the Mabira Forest in Uganda.

In my first major work (Croizat 1952) I pointed out that the range of mountains between Nigeria and Gabon is important in African biogeography. Rand (1951) considered that two barriers were active between Upper and Lower Guinea (see also Croizat 1968 a., p. 256 and fig. 31). The "centre" or node of life here is any-way very old with bonds across the Atlantic (e.g. *Utricularia*—see Croizat 1968 a.) and across Africa and intervening lands to Polynesia.

Pholidornis has been placed in numerous families, including Dicaeidae, Sylviidae, Paridae, Nectariinidae, Hyliidae, Meliphagidae and Estrildidae. There is an understandable aversion amongst systematists to very small families, particularly monotypic ones, but although not an ornithologist I do feel that if ever I ran across a genus deserving familial separation, *Pholidornis* is that genus.

The coincidence of the range of *P. rushiae* with the "centre" and the 'tracks' of, for example, the Nectariniidae—which point to the islands in the Gulf of Guinea—should suggest to the informed taxogenist that here may be a cornerstone of the dispersal and form-making of each of the families with which *Pholidornis* has been connected.

Madagascar is no better endowed with Estrildae than with Carduelinae. By contrast the islands in the Gulf of Guinea report 5 genera (out of 16, some 30%): *Estrilda*, *Cryptospiza*, *Mandingoa*, *Nesocharis* and *Nigrita*. This significant situation is paralleled in animals and plants (Croizat 1958, Vol. 1, p. 229 footnote, and Croizat 1968 a., pp. 272, 296).

Genus	No. of species	No. of races
<i>Estrilda</i>	15	51
<i>Lagonosticta</i>	8	26
<i>Uraeginthus</i>	5	14
<i>Nigrita</i>	4	13
<i>Ptilia</i>	4	10
<i>Cryptospiza</i>	4	7
<i>Ortygospiza</i>	3	13
<i>Amandava</i>	3	6
<i>Pyrenestes</i>	3	5
<i>Spermophaga</i>	3	5
<i>Nesocharis</i>	3	4
<i>Hypargos</i>	2	5
<i>Euschistospiza</i>	2	3
<i>Parmoptila</i>	1	4
<i>Mandingoa</i>	1	4
<i>Clytospiza</i>	1	1

Rather a large number of small genera. I suggest that a possible reason for this may be that the capacity for "form-making" within these genera—arising out of "old African Life"—is pretty much worn out (Croizat 1958 Vol. 1., p. 310 footnote). Laniidae have been traced back to the end of the Eocene (age of fossilization) and I would not suppose the Fringillidae, Estrildidae or Ploceidae to be younger, hence, in my sober estimation a common ancestor may easily have been extant about the mid Cretaceous.

However, as I am not an ornithologist I do not feel qualified to pronounce on the multiplication of generic types based on such factors as bill shape or tarsal scutellation.

The genus *Mandingoa* is a biogeographer's gem. Its one species *nitidula* breaks into four races. Two, *schlegeli* and *virginiae* are local, forest birds in Sierra Leone, Liberia and—after a well-known “break” (Croizat 1968 a.)—Ghana, thence to Uganda, N.W. Angola and Kasai province in southern Congo. Fernando Po is within their joint score. The other two, *chubbi* and nominate *nitidula* cover southern Ethiopia to Tanganyika (Usambara); Tanganyika (Unguru) to Pondoland and Natal inland to S.E. Congo (Katanga), Malawi and Zambia. Their joint score includes the islands of Zanzibar and Pemba. The pattern of division of Africa amongst these races is highly significant.

Although by and large neatly distributed throughout tropical Africa, the Estrildae “despatch” a lone genus beyond its confines: the genus *Amandava*.

1. *A. subflava*

A. s. subflava. Senegal to Sudan/Ethiopia and south to Nigeria, S. Cameroons, N. Congo and Uganda.

A. s. clarkei. Gabon to S. Kenya including the islands of Zanzibar, Pemba and Mafia south to Rhodesia and Mozambique.

2. *A. amandava*

A. a. amandava. West Pakistan, India and S. Nepal.

A. a. flavidiventris. Burma and S.W. China (Yunnan); Lesser Sundas (Lombok, Flores, Sumba, Timor).

A. a. punicea. Indochina, Thailand, Java and Bali; “introduced” in Singapore and Sumatra.

3. *A. formosa*. The Deccan from Gujerat to West Bengal.

The following observations are, I think, pertinent:

- i. *subflava* splits with the latitudes giving a northern and a southern race.
- ii. Pemba, Zanzibar and Mafia “open the way” to a link between East Africa and India which is not unusual.

- iii. an alternative bond may be considered with a link directly across the Indian Ocean to a point between Java and Timor out of which could have come a dispersal northward via the central plains of Thailand. This suggestion may be considered far-fetched but see my other works (Croizat 1958, 1968, 1968 b.) Chasen (1935) inferred such a link in discussing the avifauna of Christmas Island (Indian Ocean).¹ The existence of such an axis is supported by geotectonics (see Croizat 1968: 152. fig. 18). See map. 5.

The essential point is the existence of this link; its influence on different parts of the Indo-Malayan or Indonesian regions is secondary.

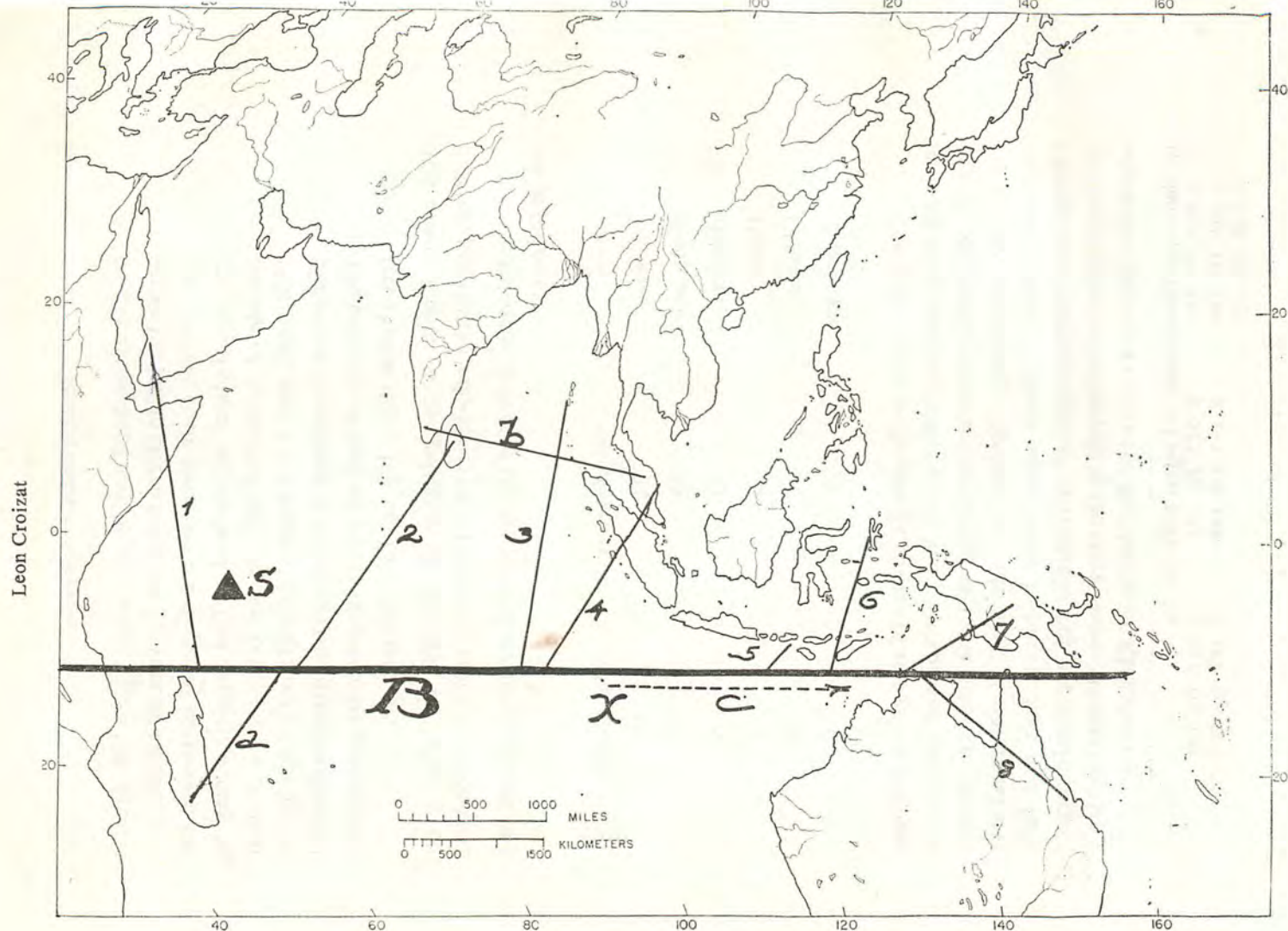
The Estrildine finches of the sub-family Lonchurae (Mannikins) are as follows :

Genus	Nos. of species	No. of races
<i>Lonchura</i>	34	96
<i>Erythrura</i>	10	31
<i>Amadina</i>	2	5
<i>Padda</i>	2	2
<i>Chloebia</i>	1	1
<i>Aidemosyne</i>	1	1

The main weight of the genetic powers of this group has been let loose in the lands between Ceylon, and Australia and the Caroline Islands, with northward extension fanning out to the Himalayas, Burma and South China through Thailand and Indochina. Only *Amadina* is confined to India. *Padda* significantly highlights Java and Bali. *Chloebia* and *Aidemosyne* appear in Australia but apparently respect the limit to distribution imposed by the MacPherson-Macleay Overlap—which also limits the southward distribution of *Rhododendron*.

1) Some specific references in Croizat 1958 Vol. 2 a.

p. 531, fig. 193	p. 532, fig. 194	p. 533, fig. 195
p. 541, fig. 196	p. 563, fig. 199	p. 594, fig. 202
p. 724, fig. 223		



Map 5. To show the main axis (B) across the Indian Ocean. Ancestral groups dispersing from a "gondwanic" landmass along this axis could have dispersed in any of the directions indicated (1,2,3,4,5,6,7,8 and a.). Transect b. across the Bay of Bengal on the other hand depicts the illusory "casual" crossing of this Bay, better explained by parallel evolution of stocks which in each case originated in the "gondwanic" landmass, but which reached the opposite shores of the Bay directly. Transect c. indicates the eastward trend of endemic avian subspecies found on Christmas Island (x). S. again marks the Seychelles.

Lonchura, with a firm base in Africa, one species occurring in Madagascar and several represented in the islands in the Gulf of Guinea and the islands off East Africa, extends eastwards. *Lonchura malabarica*, part African and part Indian has an interesting distribution. Of three races two, *cantans* and *orientalis*, are African intergrading in eastern Sudan whence *orientalis* reaches north to Arabia and south to Dodoma in Tanzania (Tanganyika); the nominate form, *malabarica*, ranges from Muscat in Arabia through Iran and Afghanistan to Nepal, Sikkim, India and Ceylon. The southern limit in Tanganyika, together with the distribution of the plant *Hypericum mysurense* (Moggi & Pisacchi 1967, p. 260) occurring in Socotra, Ceylon and the Deccan (see also *Buxus* in Croizat 1968, fig. 42) hint that in a past geological age the joint between India and Africa reached as far south as Central Tanganyika.

Lonchura occurs through Indo-Malaya and the Australasian region with an interesting crop of records from the Lesser Sundas and reaches north east to Formosa and South China. Speciation east of India and Ceylon is more widespread as if the ancestral mannikins found the area much to their liking. It is this explosion of forms which makes them by far the biggest Estrildine genus.

Erythrura is more Oriental. It occurs in the Greater Sundas and Malaya north to the classic boundary in Tenasserim (Croizat 1958) beyond which only small isolated populations occur, such as that in Loei (Deignan 1963 p. 217). Its strength lies along and to the east of an axis from the Celebes to the Philippines, thence ranging through the Moluccas and New Guinea to the islands of Polynesia though both *Erythrura* and *Lonchura* miss Australia where one or the other is perhaps represented by *Chloebia* and *Aidemosyne*.

Finally the subfamily Poephilae. The five genera rank as follows:

Genus	No. of species	No. of races
<i>Poephila</i>	5	10
<i>Emblema</i>	4	4
<i>Neochmia</i>	2	5
<i>Aegintha</i>	1	3
<i>Oreostruthus</i>	1	3

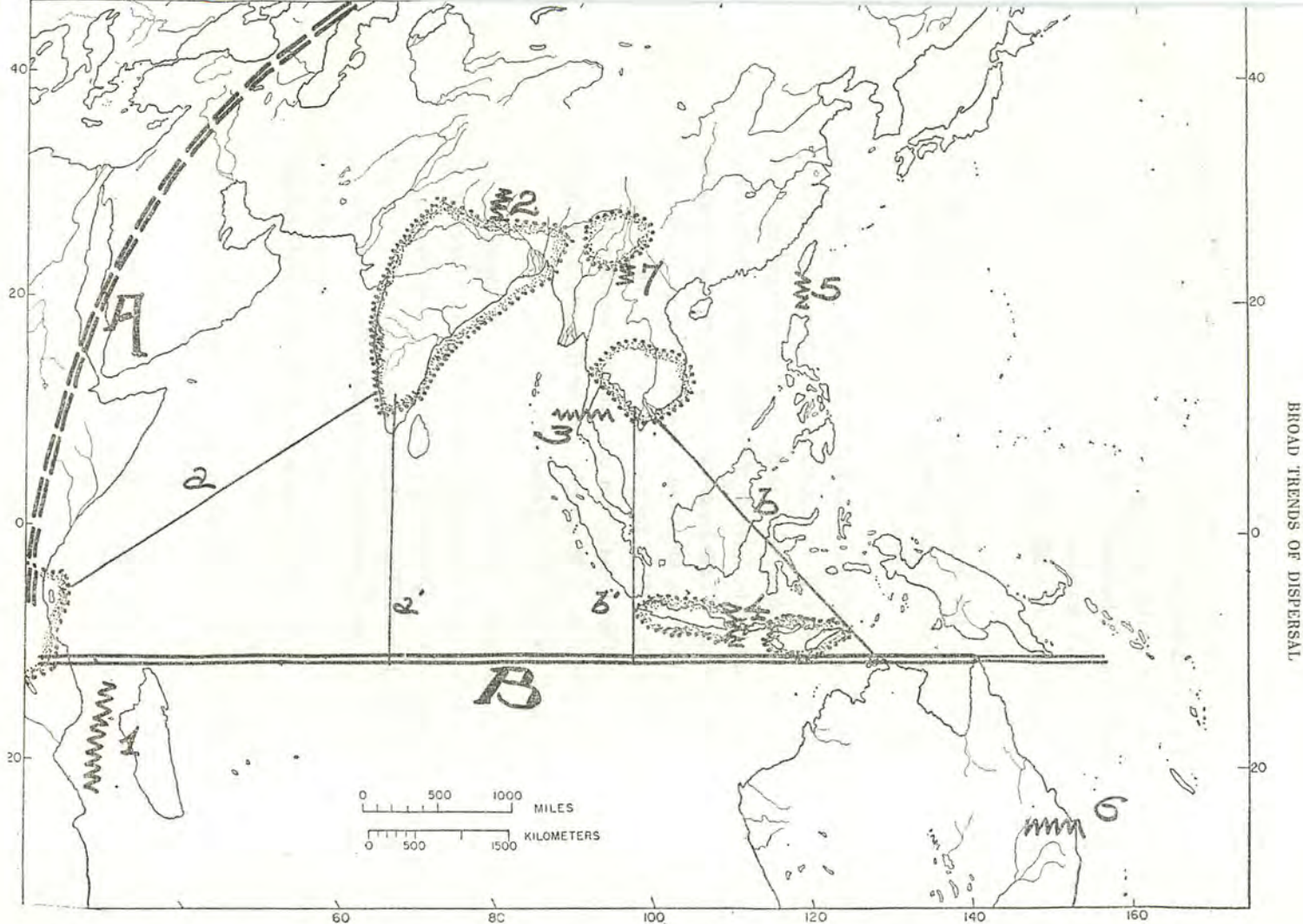
Aegintha is wholly Australian with the weight in the east.¹ *Emblema* is also Australian but chiefly from the south and centre. *Neochmia* ranges from southern New Guinea and Northern Australia down each coast. *Oreostruthus* is confined to New Guinea. *Poephila* has three Australian species in the nominate subgenus but the subgenus *Taeniopyga* with two species, although almost wholly Australian, has a single race *P.g. guttata* endemic to the islands of the Lesser Sundas, from Lombok to Timor and nearby islands.

This then completes my review of the Fringillidae, from which I have excluded *Fringilla* though its records would not influence my conclusions, and the Estrildidae: a considerable body of birds between them occurring in the five continents.

What we may conclude from this I will try to summarise in the accompanying map (Map 6.) and in the following comments:

1. Africa is clearly the keystone of the distribution of these groups, the point whereat would have occurred a common arch-ancestor not later than about mid-Cretaceous. Africa is used once again in the sense of a part of the as yet unsundered Gondwanic landmass. In the break-up of this landmass the opening up of the Mozambique channel towards the mid-Jurassic is of the utmost importance in biogeography on account of its timing.

1) The student of Australian biogeography may find my paper on *Eucalyptus* (Croizat 1967) interesting though the editing leaves much to be desired.



Map 6. To show the main trends of dispersal in the Fringillidae and Estrildidae. Broadly the Fringillidae follow track A. and the Estrildidae track B. The stippled borders enclose the known distribution of *Amandava*, and the existing dispersal probably involved "tracks" a/a' and b/b'. The zig-zag lines depict biogeographic landmarks as follows:

- | | |
|-----------------------------------|---------------------------------|
| 1. Mozambique Channel | 5. Balintang or Babuyan Chennel |
| 2. Sikkim | 6. MacPherson/MacLeay overlap |
| 3. Tenasserim/Prachuap Khiri Khan | 7. Khun Tan Range. |
| 4. Wallace's line. | |

2. Out of this Africa then the ancestral stock of the Fringillidae streamed northwards veering east to eventually reach the new world, avoiding warmer Asia and Malaysia to Australia. The clear trend of the dispersal argues against climate and chance as reasons in this distribution, and the Fringillidae are well represented in the tropics in Africa and America.
3. By contrast the ancestral stock of the Estrildidae moved eastward towards India, Malaysia, Polynesia and Australia.
4. The sweep and clearness of these dispersals, together with the subsequent form-making in all taxonomic brackets, suggests that the original radiation of these ancestral types can have been no later than the end of the first part of the Cretaceous. These ancestral types carried with them the potential to form what today we recognize as *Carduelis* or *Estrilda* etc. That they did carry this is not simply a hypothesis for had this not occurred one would not today find fringillids in Patagonia and the Congo and estrildids at the Cape and in the Palaus and Samoa.
5. It is glaringly false to suppose that Madagascar, for example, was "colonised" through chance dispersal or "sweepstake" (Croizat 1968 p. 207, fig. 23); as evidence of this the Fringillidae although abundant in Africa are absent from Madagascar and the Estrildidae scarce. By the same token "double invasion" cannot be held to account for the form-making in the islands in the Gulf of Guinea (Fernando Po, Principe, Annobon etc.).
6. The statistical analysis of these groups has in no way contradicted the conclusions drawn from *Otus* and *Corvus* and dispersal can be said to follow broad principles in an orderly fashion. This itself permits the analysis we have employed.

7. It is true that "ecology" is an important consideration throughout and that the Estrildidae, for example, are always found in comparable environments. That this factor is secondary is, however, demonstrated by the Fringillidae and the Estrildidae which could be expected to mingle wherever "ecology" and "climate" were suitable, and should be found together today wherever these conditions were still suitable. By contrast the original Cretaceous dispersal of these groups was along definite trends which led to the establishment of ancestral groupings in different centres, then the descendant forms evolved virtually *in situ* under the influences of climatological and ecological considerations, which certainly affected their survival and further evolution. This is equally true of plant life and for this I submit as evidence the analyses undertaken in the 8,000 or more pages of my main works.
8. Again I would stress that the concepts of "chance" dispersal or storm-driven emigrants have been raised without allowing for the effects of time, over which the landmasses which witnessed the basic dispersals have changed so much that the maps of today, even with their continental shelves etc., may mislead. Such concepts of dispersal do not explain the movement of Fringillidae from Africa to Central Asia to Venezuela, of *Picumnus* from Brazil to Borneo, of *Iguana* from Mexico to Madagascar and Tonga, or of *Lonchura* to the Palaus.
9. It is obvious that the main massings of life established during the original radiation have been in part modified by subsequent geological and climatic events; but the suggestions of broad movements correlated therewith, e.g. *Lonchura* "emigrating" to Yakutia when it became "warmer" or *Carpodacus* to Australia when it became "colder", do not seem tenable on account of contradictions.

10. **Deignan** quickly appreciated the argument that since zoological classification is based upon orderly form-making the science of dispersal could not and should not rely upon chance. His acceptance of my conclusions as being constructive and not in conflict with ornithological data was demonstrated by one of his last papers (Deignan 1963 a.).

Having recapitulated let us now examine the Ploceidae. Many authors persist in associating the Ploceidae with the Estrildidae and taxogeny suggests that they cannot be very wrong.

Following once more the Check-list we find that the Ploceidae consists of 4 sub-families: the Viduinae which is monogeneric, the Bubalornithinae with two genera and Passerinae and Ploceinae with eight genera each. The overall generic ranking is as follows:

Genus		No. of species	No. of races
<i>Ploceus</i>		57	125
<i>Euplectes</i>	A	16	51
<i>Passer</i>		15	57
<i>Malimbus</i>	A	10	18
<i>Montifringilla</i>		7	15
<i>Foudia</i>	A	6	11
<i>Petronia</i>		5	13
<i>Plocepasser</i>	A	4	9
<i>Vidua</i>	A	3	9
<i>Quelea</i>	A	3	6
<i>Pseudonigrita</i>	A	2	4
<i>Sporopipes</i>	A	2	3
<i>Amblyospiza</i>	A	1	10
<i>Philetairus</i>	A	1	4
<i>Bubalornis</i>	A	1	3
<i>Dinemellia</i>	A	1	2
<i>Histurgops</i>	A	1	1
<i>Neospiza</i>	A	1	1
<i>Anomalospiza</i>	A	1	1

It may be seen at once that *Ploceus* represents some 40% of the total species and 36% of the total number of races. It is also notable that the ratio of races to species is low—about 2 : 1—and indicative of the taxa being rather “worn out”, despite an abundance of favourable ecological niches. **Rand in Peters** (1968) comments in a footnote on page 231 on *Neospiza Salvadori* 1903 (which has the distinction of appearing in **Peters** Vol. 14 as a fringillid and in **Peters** Vol. 15 as a ploceid): “probably related to the African carduelines (see **Amadon**, 1965, *Ibis*, pp. 395-396)”; that such a ‘link’ species should exist in Sao Tomé in the Gulf of Guinea is no surprise to the biogeographer and taxogenist.

The genera of the African region are listed with an “A” in the above list and will be seen to represent about 80% of all the genera. Of these *Foudia* is endemic to Madagascar and islands in the Indian Ocean and apart from this genus, the ploceids are represented in Madagascar by only two species: *Ploceus nelicourvi* and *Ploceus sakalava*—the former monotypic, the latter has two races. Of the six species of *Foudia* five are monotypic, the other—*eminentissima*—has six races. By comparison we have seen that in Madagascar the Fringillidae are unrepresented and the Estrildidae represented by one species: *Lonchura nana*. These low scores must be compared with the wide ranging of these families over three continents and one must then acknowledge that the scores are too low for chance dispersal to be acceptable. The truth is that we do not know what obstacles could have debarred the ancestors of certain plants and animals from what was to become Madagascar. Arms of the sea, deserts or high mountains could have intervened during the Triassic/Jurassic and the earliest Cretaceous but 140-180 million years later we do not know what these obstacles were, nor why the ancestors of the Piciformes, for example, were debarred, yet the ancestors of the Vangidae, of *Foudia* and of certain “timaliine/pycnonotid” birds were admitted (see **Salomonsen** 1934).

Ploceus reaches Asia with but 5 species and is Indo-Malayan for less than 9% of its total speciation. By contrast its mass in Africa yields a most instructive crop of records; these I will not examine here in detail, suffice it to say that the islands in the Gulf of Guinea and the coasts of the nearby mainland are characterised by a number of monotypic species. *Malimbus*—except for *M. rubriceps* which is a classical “eastern” species—adds a virtually perfect “western” score of the kind examined above. In sum there can be no doubt that one is here right in the heart of the area of archetypical form-making of the pre-Fringillidae, pre-Estrildidae, pre-Ploceidae and the pre-Nectariniinae etc., indeed one of the cradles of the passeriformes, perhaps even the ultimate cradle for the world at large.

Montifringilla and *Petronia* follow a course that by now should not surprise us. *Petronia* can be “picked up” north of Tanganyika and of the Niger Republic and from the area Arabia/Iraq/Iran; from these limits it stretches north into the Canaries, Madeira, N. W. Africa and Europe to Eastern Siberia, Mongolia and China south to the Himalayas. South of the line Niger to Tanganyika is *P. superciliaris*, occurring south to the Cape, and *P. dentata* which runs from S.W. Arabia, Eritrea and the Sudan west to Senegal linking the Arabian and West African elements. *Montifringilla* to the biogeographer is an extra-African montane edition of *Petronia* occurring from the Zagros mountains in S.W. Iran north in Europe and the Himalayas and north of them abounding in the mountains of Central Asia and Western China. The distribution of these two genera is essentially of the fringilline type, though failing to reach the New World.

Passer, the last ploceid genus on our list, is peculiarly interesting but before examining it I must digress and consider the dispersal of *Pyrrhula*, a fringillid which I purposely omitted earlier. Due to lack of records my mention of this species (Croizat 1958, Vol. 2a, p. 438 et seq.) has been brief.

Voous (1949) mentions amongst the allies of *Pyrrhula* the “American goldfinches and purplefinches” and Paynter in Peters (1968) footnotes the genus *Pyrrhoplectes* “A distinctive genus usually placed

near the bullfinches but there is no evidence or even indication that they are closely related. It may not even be a cardueline." *Pyrrhula* then is no less challenging to the biogeographer than is *Pyrrhoplectes* to the systematist and I find it not improbable that *Pyrrhula* is involved in phylogeny with *Rhynchostruthus* and *Rhodopechys*.

Of the six species of *Pyrrhula* two raceless ones are essentially Himalayan: *aurantiaca* and *erythrocephala*. The Himalayas also figure in the ranges of two other species. *P. nipalensis*: mountains of Malaya (Perak, Pahang and Selangor), Burma (Mt. Victoria, the Adung Valley etc.), and the Himalayas westward to Gilgit in northernmost West Pakistan and eastward to S. China, N. Tonkin and Taiwan. *P. erythaca*: Taiwan and S. China westward along the Himalayas to Sikkim.

These records suggest that the bullfinches "invaded" the Himalayas from the direction of Malaya and having reached the latitude of northern Burma they fanned out and differentiated.

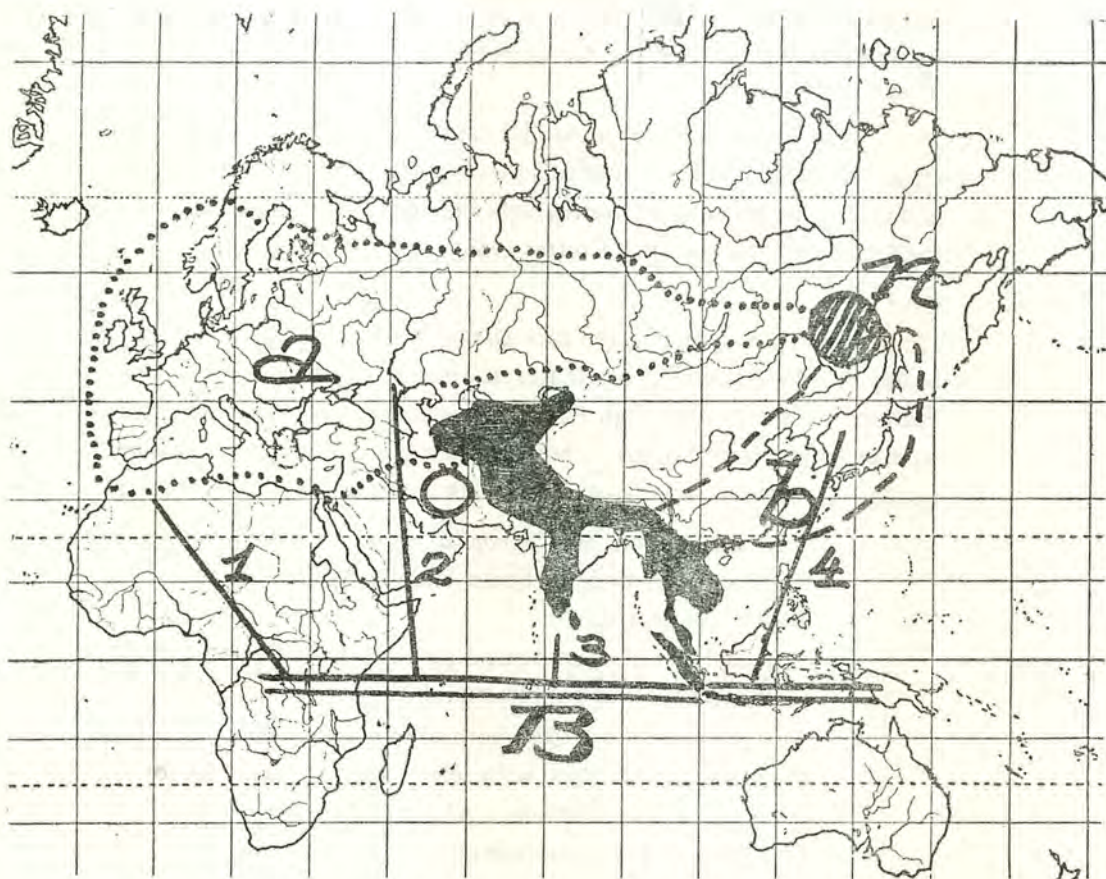
A fifth species, *P. leucogenys*, found in the mossy forests of the Philippines (Lepanto in N. Luzon and Mt. Apo in Mindanao) is probably an offshoot of this same "stream of migration".

This leaves us with *P. pyrrhula*. Two races occur in Iran: *caspica* and *rossikowi* and from here the species fans out eastward on the front Kamchatka, Kuriles, Japan and westward to the front British Isles, Iberian Peninsula, Azores. It is not found in the Himalayas: the race nearest to India is *cineracea* in the northern Altai and the Sayan Mountains on the shores of Lake Baikal, with *caspica* on the southern shores of the Caspian Sea about equidistant. The nominate species indeed seems to be isolated from the conglomeration of its congeners. I have commented elsewhere (Croizat 1962) on the views of Dobzhansky et al. on the dispersal of *Parus*. These comments led me to a visualisation of the Aralo-Caspian region as a very important centre of avian evolution and dispersal to west, north and east thereof. Ancestral *Pyrrhula* certainly seems implicated in this centre but its "track" through Malaya to the Himalayas, which is paralleled by that

of *Primula*, brings one to the conclusion that, like *Otus* which we discussed earlier, its evolution has been bicentric.

The representative of *Pyrrhula* in the Azores is sufficiently well-marked that Voous (1949) treats it at specific level as *P. murina*, though others disagree and prefer to retain it as a race of *Pyrrhula pyrrhula*. Both sides however agree that *Pyrrhula* reached the Azores as a casual straggler from Europe, and with this I would take issue. In my considered opinion *Pyrrhula* "invaded" the Azores in ages long past when they certainly looked different on the map. Two plants, *Myrsine africana* and *Euphorbia stygiana*, seem parallel cases in respect of the Azores and other evidence of a similar nature is abundant. *Pyrrhula murina* then evolved out of ancestral stock in the Azores, *P. pyrrhula* evolved west of the Himalayas and out of a third centre evolved the ancestor of four species now found in the Himalayas and a fifth in the Philippines. Voous believes that the "centre of origin" of *Pyrrhula* is to be sought in the Chinese-Burmese region. I would agree that this region may be one of the "gates" of the Bullfinch but would not let the matter rest there. Indeed Voous highlights a number of important points: firstly, that the oriental and himalayan species form a taxonomic unit to the exclusion of *P. pyrrhula*, indeed he suggests *P. nipalensis* as "prototypical" which however questionable does draw attention to the track Malaya/Assam; secondly he underlines the confused status of the populations in Siberia which he refers to *P. pyrrhula*, *P. griseiventris* and *P. cineracea* in which he sees "emergent interspecies"; and thirdly he points out the similarity of the general distributional behaviour of *Pyrrhula* and *Dendrocopos* in those regions.

To me the truth is simple. Whenever populations of the same taxon (e.g. genus or species) meet at the extremity of ranges rooted in different "gates"—such as the Near East and Malaya in the case of *Pyrrhula*—"quirks" of taxonomy or dispersal arise which, not hard to visualise for the taxogenist or biogeographer, are made unwieldy by the straight-jacket of formal classification. Examples of such quirks are the refusal of "obvious races" to interbreed when they overlap



Map 7. To show the dispersal of *Parus major* (a-boundary dotted), *P. minor* (b-boundary broken) and *P. bokhariensis* (solid black range). A problem zone, where "races" occurring defy systematic treatment, lies just north of "O". The shaded circle "N" marks the eastern limit of similar problems attending the case of *Pyrrhula*. The axes 1, 2, 3, and 4 arising out of main axis B. indicate the probable dispersal out of a common origin in a fashion that would explain the problems of their behaviour when different groups meet. See Dobzhansky (1951), Vaurie (1950) and Delacour (1951).

(Croizat 1962, p. 505 et seq.) and the occurrence of "emergent interspecies"—common in certain ranges—and similar phenomena which each author understands in ways that suit him despite a general lack of agreement.

Map 7. demonstrates a parallel case to *Pyrrhula*—bicentrism in *Parus*. It demonstrates that one of these ranges in which quirks occur is bound to lie broadly within the area between Western Siberia and the Sea of Okhotsk (see also Croizat 1958; 2a; p. 258, fig. 148 and p. 332 fig. 163).

Also noteworthy is the fact that the track of *Pyrrhula* from Malaya to the Himalayas originates at a spot significant for its connections with Africa through *Ploceus*, *Amandava* and other taxa and whence has arisen *Serinus estherae*. Let the champion of chance ponder this and let him also explain a few facts which puzzle others:

1. The distribution of *Cyanopica cyana*: the magpie with isolated populations in Spain and Transbaikalia/Southern China. Bicentrism?
2. The existence of certain puzzling birds in the Celebes which look like ancestral babblers might be expected to look.
3. The presence of the Cercopithecine monkey genus *Cynopithecus* in the Celebes with clear relationships to fossil monkeys of East and South Africa and to live monkeys of Ethiopia and the Cameroons.
4. The relationships between *Pavo* and *Afropavo*.
5. The abundance of babblers in Thailand compared with the virtually complete lack of Fringillidae, except for one resident *Mycerobas*.

Finally it should not be forgotten that the fundamental trends of dispersal that I have outlined have undergone secondary modification due to the extent of glaciation in the later Ice Ages. Voous, for example, is well aware of this factor but understandably finds it hard to extricate this secondary influence from the primary influences, a separation which is eminently desirable to keep the record clear.

To return at last to *Passer*. *Passer* strikes me as "bicentric" along the lines of *Pyrrhula*. A number of African species lead smoothly into the forms of *Passer domesticus* which are centred west of the Himalayas. On the other hand species like *flaveolus* and *rutilans* together with certain other races of *Passer domesticus* are distributed in such a manner as to suggest direct oriental origins. It seems unlikely to a student of dispersal that the whole of Eurasian *Passer* is bound with only one end of the east-west axis (b. in map 2.). This incidentally applies equally to *Parus "major"*, as understood by Peters's Checklist.

Hence the Ploceidae also fit the concepts that we first suggested and throw up no facts which firmly contradict the broad patterns of dispersal which have taken place over time.

C. ON "TRANS-ATLANTIC" DISPERSAL

I have previously analyzed dispersal which runs, in the main, eastward from Africa and I feel bound to comment also on dispersal from Africa westward to the New World.

Unfortunately the volumes of Peters's Checklist dealing with Emberizidae and Sylviidae are not yet to hand so I must leave for a later date the buntings of Tristan da Cunha and certain "Sylviidae" (see Croizat 1958: 2a. p. 85 et seq.) and also *Anthus* in general and *Anthus antarcticus* in particular (Croizat 1958: 1; p. 309 et seq.). In passing however I would draw attention to the case put by Rand & Taylor (1953) for the American genera *Polioptila*, *Microbates* and *Ramphocaenus* and the African genus *Macrosphenus* (which is basically western—with a record from Fernando Po) being distributed transatlantically.

Many years ago Peters himself brought to my attention a classical case of Afro-American distribution: *Ciccaba*—a strigid owl is credited with the following distribution:

1. *C. woodfordii* :

- a) *C. w. umbrina* : Ethiopia to E. Sudan (Boma Hills).
- b) *C. w. nigricantior* : E. Congo to Uganda, Kenya, S. Somaliland, Tanganyika.
- c) *C. w. nuchalis* : Sierra Leone eastward to the Cameroons and Uganda, southward to Angola.
- d) *C. w. bohndorffi* : Ubangi-Chari eastward to S. Sudan (Didinga Mts.) southward to the Congo (Kasai) and Angola.
- e) *C. w. woodfordii* : Angola to S.W. Tanganyika, Nyasaland, Mozambique, Zambia (N. Rhodesia) southward.

This is a classical distribution for a forest bird with eastern, western and southern populations and central connecting links. The ancestors of this owl in Africa were certainly there no later than those of, for example, *Struthio*.

But *Ciccaba* continues as follows :

- 2. *C. huhula* : Guianas, Brazil (north of São Paulo), Colombia (Meta).
- 3. *C. albitarsus* : Venezuela (Trujillo, Mérida) (Phelps and Phelps 1958), Colombia (Cundinamarca, Tolima, Caldas, El Valle) Ecuador (north of Quito).
- 4. *C. nigrolineata* : Venezuela (rather local in the Caracas area, Aragua, Miranda, Guárico, Zulia (Perijá), Colombia (Santander, Cundinamarca, Huila, Tolima, El Valle—not in Narino) westward to Mexico (Oaxaca, Vera Cruz) and through Central America.
- 5. *C. virgata* :
 - a) *C. v. borelliana* : southern Brazil, Paraguay, N.E. Argentina.
 - b) *C. v. superciliaris* : Brazil (lower Amazon basin : from the Guaporé and Madeira to Pará).

- c) *C. v. macconnelli*: Guianas, Venezuela (Bolívar, Terr. Amazonas), Colombia, (Caquetá), Ecuador.
- d) *C. v. minuscula*: Colombia (Chocó) to W. Ecuador.
- e) *C. v. virgata*: Trinidad, Venezuela (Delta Amacuro, Monagas, Sucre, Aragua, Lara, Táchira, Zulia), Colombia (Magdalena, Antioquia), Panama (to the Canal Zone) and Ecuador.
- f) *C. v. centralis*: W. Panama through Central America to Mexico (Yucatán and the southern and eastern states to Vera Cruz). (Blake 1953).
- g) *C. v. squamulata*: Mexico (Mexico D.F., Morelos, Guerrero to S. Sonora and Chihuahua).
- h) *C. v. tamaulipensis*: Mexico (southern Nuevo León, Tamaulipas).

I would suggest that the ornithologist who is familiar with the birds of the New World will find this distribution well defined and well-knit. Now *Ciccaba* is a generally sedentary forest owl and yet its distribution is such that the Atlantic might just as well not exist.

The strigid genera *Jubula*--ranging from Liberia to the Cameroons and the Congo--and *Lophotrix* ranging through tropical America from Brazil to S. Mexico--have at times been lumped. From the biogeographers viewpoint this then parallels the case of *Ciccaba*.

The science of geophysics has provided precise information as to when Africa and the New World became separated (Heirtzler 1968). This is put at about 150 million years ago which in no way contradicts the views put forward on biogeographical grounds throughout my works.

I cannot believe that an order as widely distributed as the Strigiformes, and which clearly has roots in common with the Caprimulgiformes, was not widely distributed, in an early ancestral form, by the late Jurassic or early Cretaceous. And this I think is not belied by palaeornithology especially once one has grasped that *age of fossilization* is by no means the same as *age of origin*.

The inescapable conclusion is that the ancestral stock of *Ciccaba* was already dispersed and over a landmass which was later to come apart leaving elements of this stock on each shore of the gradually widening Atlantic. Dispersed then more than 150 million years ago. The same conclusions apply on a broad scale—*Euphorbia* ancestors were already dispersed even earlier and prior to the separation of Madagascar and Africa; the ancestors of *Erica* and *Rhododendron* were also dispersed in such a way that their presence in South Africa and the Far East/Malaysia represents ground held onto, footholds never lost.

Why does conventional zoogeography fail to provide concrete answers to problems of this kind? I would suggest that:—

1. it lacks a proper method for the analysis of actual records of distribution:
2. it fails to understand that life and the earth itself evolved together: particularly the inter-relationships of, for example, geology and the evolution of life are little appreciated;
3. its chronological workings are erroneous—events being supposed to be far too recent.
4. its grasp of the mechanics of form-making through time and over space is weak.

Now it will be pointed out that 'casual' transatlantic dispersal is in a recent case—that of *Bubulcus ibis*—positively proven. True. I am not saying that such dispersal is beyond the possibilities of chance: rather that chance is invoked far too often for lack of the effort to seek the real truth.

There was no need for a chance flight over the Atlantic by *Ciccaba*, as, when its ancestors spread out, no Atlantic existed to deter them. The broad facts of distribution which can be analyzed or mapped tell a story—which is sufficiently broadly based to be statistically reliable.

The breadth of this base is in want of appreciation because the trends of scientific thought and training have left very few naturalists who have:

- a) the quantity of data on the distribution of taxa marshalled and ready for study, *and*
- b) a wide grasp of the geography of the world as a whole—its districts and its place names, which, if known, spin the memory banks of the brain and produce, almost intuitively, the broad and revealing correlations to be analyzed for probability and for cause and effect.

D. ON THE DISPERSAL OF THE EMERALD CUCKOOS

Ornithological literature has been enriched recently by the detailed work on *Chrysococcyx* by **Friedmann** (1968). Considering the difficulty of establishing the ranges, both resident and migratory, of Cuculicae in general, this work is of the greatest biogeographic significance.

Friedmann remarks that the seasonal migrations of *C.l. plagosus* and *C. l. lucidus* "suggest a revealing annual retracing of their ancient ancestral dispersal between their present southern (South Australia/Tasmania) and south-eastern (New Zealand) breeding areas and their original "locus of origin". Undoubtedly *Chrysococcyx* did reach Australia from the north-west in an ancestral form. The genus is distributed from Africa to the south-western Pacific and no one has claimed a Pacific origin for it—**Friedmann's** "locus of origin" lies inferentially between Malaysia and Western Africa.

One also learns from **Friedmann** that although *Chrysococcyx*, *Cuculus* and *Cacomantis* form natural groups their similarities are great, and a common ancestor is indicated, although "the genera...are ancient and, as so often happens in such categories, some have differentiated in the directions of the others making it very difficult at this late date to distinguish between original similarities or differences and later convergences or divergences". This indeed characterises the recombination of ancestral characters which is the key to form-making over space through time.

Exactly the same is true of plant life (Croizat 1968 a., p. 345 et seq.) for the basic laws of dispersal and form-making are true of both plants and animals.

Friedmann has not given particular attention to the islands in the Gulf of Guinea upon which, in relation to *Chrysococcyx*, I commented earlier (Croizat 1958, 2a, p. 654 footnote) and to which I should now like to return.

Friedmann's group C. contains the following species: *C. flavigularis*, *C. klaas*, *C. cupreus* and *C. caprius*. The ranges of these and their subspecies may readily be analysed using Friedmann (1968) or Peters Vol. IV, pp. 29-30 (1940). Amongst these, *C. flavigularis* stands out: it shows the classic western range associated with plants and animals of the heavy forest from Sierra Leone to Uganda. Such distribution may or may not include one or more islands in the Gulf of Guinea; in the case of *C. flavigularis* it does not, though the other three species occur there, but in *Dicrurus adsimilis*, for example, it does (Vaurie 1949).

Friedmann does give close attention to *C. flavigularis* which he judges to be nearest "to the original...stock..." and says of its range "most of the Asiatic 'relicts' in Africa are found in precisely that area" (though he says this in the context of a discussion of the bird's descent from "an originally South Asiatic stock").

Superficially the ranges of the other three species are similar. However a closer examination does reveal differences and these remind me of the genus *Cercococcyx* and of the species *Alcippe abyssinica*. In the latter the distribution is composed of western, central and eastern elements, all montane. There is considerable isolation but great alterations of distribution may take place even within a short time-span because of climatic change (Croizat 1952, p. 339). In Africa, to give one example, the fluctuating limits of the "Sahelian" zone—both at its north and south edges are answerable for relicts of plant life stranded today in "dry" or "wet" Africa in a remarkable fashion (Croizat 1962, p. 220 et seq.). The apparently peculiar distributions that result today from this are often ascribed to chance.

My impression is that *C. cupreus* is basically western, *C. klaas* essentially eastern, whilst *C. caprius* might be central. **Friedmann** postulates a close relationship between *C. flavigularis* and *C. klaas* and as a student of dispersal, noting that the two complement each other geographically and ecologically, I find this highly probable.

Friedmann calls the species *malayanus*, *basalis*, *lucidus* and *osculans* "the older stock of the genus".

That *C. malayanus* has a plumage pattern reminiscent of *Cuculus* has caused the suggestion that *malayanus* is the "oldest" species in the group. I would submit however that having reached in Australasia the farthest end of its range it is normal that it should have retained archaic features. However in discussing the plumage of *C. flavigularis* **Friedmann** notes that "it forms a significant link between the two sections of the genus" i.e. the African and the Malaysian-Australian. This point is made concerning the ventral barring in the female to which **Friedmann** returns, when he finds this suggestive of *Cacomantis*, and raises the possibility that "*Cacomantis*, or some similar stock may have been the remote ancestor..." On the whole however he concludes that this feature is suggestive of proximity to *xanthorhynchus* and *maculatus*, with this pair of species representing an intermediate stage of evolution out of *malayanus*. The conflicting resemblances to *Cuculus* and *Cacomantis* taken together with the points at which these occur suggest that the plumage patterns may not be a very reliable guide to the evolutionary history of the group.

The discussion of this generic evolution has proceeded in isolation from the consideration of similar patterns in birds found common to the various areas. Thailand lists three species of *Chrysococcyx*—*maculatus*, *xanthorhynchus* and *malayanus*. These may be related in the fashion employed by **Friedmann**, but at the same time other taxa show patterns which have been presumed to have very different links—*Pavo* with *Afropavo* in the Congo. *Hypsipetes* with other *Hypsipetes* in Madagascar, *Dendrocopos* with congeners in the Himalayas etc. etc. The patterns exist and are factual and I do not

believe that analysis of them will yield positive results until a common demoninator is accepted and a method is employed which in each case accepts the same basic precepts of evolution and form-making under the forces of space and time.

The specialist in a genus has a most important task but he is in no way assisted by the plethora of differing zoogeographical explanations for different taxa evolving against the same backcloth.

Would you then say that a biogeographer is a generalist? I would not. I would consider it most definitely a speciality—a precise science in its own right. Its precision is to be demonstrated by its ability, not to find different solutions for different taxa, but to piece together the series of factors which over space and time have affected different taxa in like ways. The naturalist who fails to perceive this and adds to the 'plethora' of zoogeographic "explanations" which clutter up the textbooks performs a disservice to his ultimate cause. The situation indeed has reached a bottleneck stage with the obstructions of such theories—taken as facts—holding up the advance of biology.

Moreau and Chapin (1951) dealt with *Chrysococcyx* and the distribution on the islands in the Gulf of Guinea. These islands are, I would repeat, of major importance. Rand (1951) mentions that some 40 years ago Chapin visualised that a former submergence of the land near the present Niger delta might account for the break between the Upper and Lower Guinea forest. In fact both geology and plant distribution confirm that "Afro-America" broke off hereabouts some 140 million years ago and this must have been accompanied by gradual sinking and the creation of ecological and evolutionary paradises in and around the mangroves for plants and animals. To me it is suggestive that *Chrysococcyx xanthorhynchus*—a close relative of *C. flavigularis*, as Friedmann agrees—occurs in Borneo as follows: "sparingly distributed in the lowlands, and found in gardens in Sarawak, *on the edge of the mangrove swamps, and on the seashore*" (italics mine). Borneo is the paradise for "mangroves" that have extended inland (Croizat 1968, p. 179 et seq.) and the home of an

avian relict—*Pityriasis gymnocephala*—which associates particularly with “peatswamp forests” (Smythies 1960).

The islands in the Gulf of Guinea are, I believe, the remnants of a rich and extensive area which was the cradle, and often the graveyard, of an immense amount of animal and plant life.

Moreau & Chapin tabulated the tail lengths of different *Chrysococcyx* populations and found that in the islands in the Gulf of Guinea they averaged shorter than those of birds living on the adjacent mainland, and also that this feature showed a trend towards southern Africa. Although this should be interpreted by an ornithologist I find it suggestive of the same underlying events as the distribution of the ploceid *Euplectes aureus*. This weaverbird occurs in coastal Angola and in S. Tomé island. Some, of course, will suggest that by chance the wind blew it from Angola to S. Tomé or vice versa. I cannot agree; the sum of the evidence is for dispersal out of the area now marked by the islands in the Gulf of Guinea.

E. WHICH GENUS FOR A WOODPECKER ?

There is a small woodpecker with the specific name *obsoletus* ranging through Africa with a related form in Arabia with the name *dorae*. Bannerman (1953) and Cave and Macdonald (1955) place it in the genus *Dendropicos*. Meinertzhagen (1954) places *dorae* under *Dendrocopos*. Mackworth-Praed and Grant (1957) place it under *Ipophilus*. Voous (1947) considers *obsoletus* taxonomically quite close to the “south Indian” *nanus*; *nanus* he conceives as a grouping of the races occurring from Ceylon to the Himalayas east to Nepal and East Pakistan. Ripley (1961) widens *nanus* to include forms from “the Malaysian subregion and the Lesser Sunda Islands.” Both these authors place these birds in *Dendrocopos*.

In the standard Russian work (Dement'ev & Gladkov 1951) *nanus* is placed in the genus *Jungipicus* (sic) together with *kizuki*. The former is distributed from Sumatra, Borneo and Malaya north to Nepal, through Indochina, Hainan, Taiwan and China to Korea, Manchuria and Primorie to about the latitude of southern Sakhalin.

J. kuzuki is sympatric with *nanus* in Korea, Manchuria and Primorie: and is endemic to the Riukius, Japan, the islands between Japan and Korea, the southern Kuriles and Sakhalin.

Peters (1948) disagrees. He places *nanus* with *moluccensis* and gives the range of the latter as Ceylon, India, Malaya, Sumatra, Riouw archipelago, Natuna Islands, Billiton, Borneo, Java and the Lesser Sundas east to Alor. He does accept *kizuki*, genus *Dendrocopos* as for *moluccensis*. The bulk of the races assigned to *nanus* by the Russians (except *nanus* itself) he assigns to *D. canicapillus*, which thus ranges from Sumatra north to the Primorie.

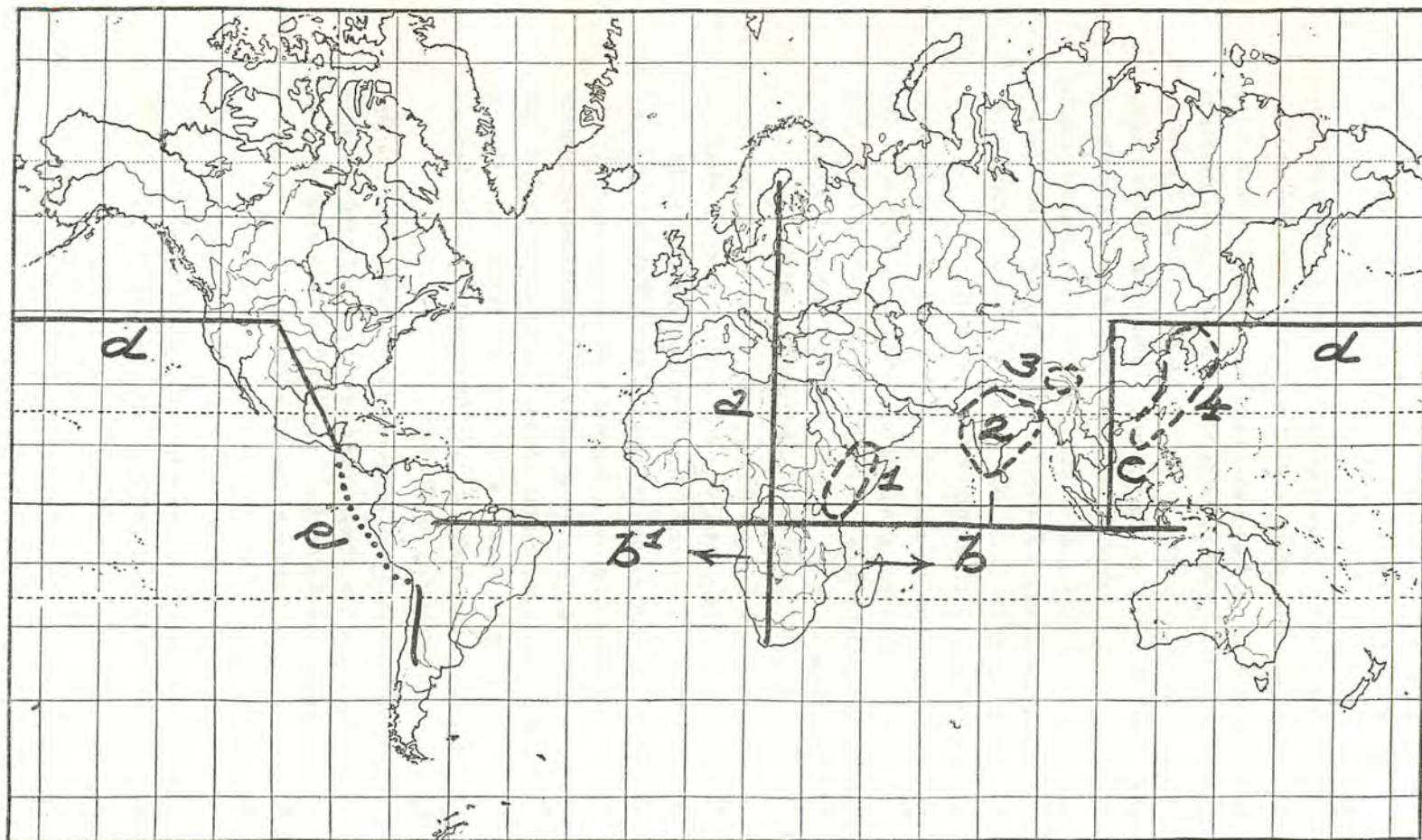
Incidentally Thailand lists 4 races of *canicapillus* (Deignan 1963), and these are, one might suppose, of "southern" origin. The remaining *Dendrocopos* taxa of Thailand:

- D. cathparius tenebrosus*
- D. hyperythrus hyperythrus*
- D. hyperythrus annamensis*
- D. atratus*
- D. macei longipennis*
- D. mahrattensis*

have Himalayan affinities, though *macei* has links with Java and Bali and may also be "southern".

D. mahrattensis is of interest. Voous (1947) considered it so distinct that it could almost be treated as a genus of its own, *Leiopicus*, and added "It probably represents one of the rare autochthone bird species of the Gondwana Continent whence it has spread in a northern and north-eastern direction." Now Voous related this to the Tethys, and Ripley (1949) faulted this on timing—though only of its physical existence and not on the timing of the effects of its existence.

Anyway the taxonomic status of these small woodpeckers—both at specific and at generic level—is highly contentious. I have stressed before (Croizat 1962; p. 500 et seq., in particular p. 516 on) that often the fundamental unit of taxonomic thought is *not* the species but the subspecies or race. The dissent over what constitutes a good race is



Map 8. To show the dispersal of *Dendrocopos*. It is virtually along axis *b*, that occur the controversial genera: 1. *Ipophilus*; 2. *Leiopicus* and *Hypopicus*; 3. *Picoides*; 4. *Yungipicus* (ranges shown are diagrammatic and not complete). *Dendrocopos* "tracks" cross the Pacific (axis *d*) to the New World and continue south to Latin America though with a large discontinuation (*e*). Axis *b¹* across the Atlantic links *Campethera* to the New World. See text p. 306.

invariably less strident than the dispute over the allocation of races, each well accepted, to species. What are "valid" specific limits?

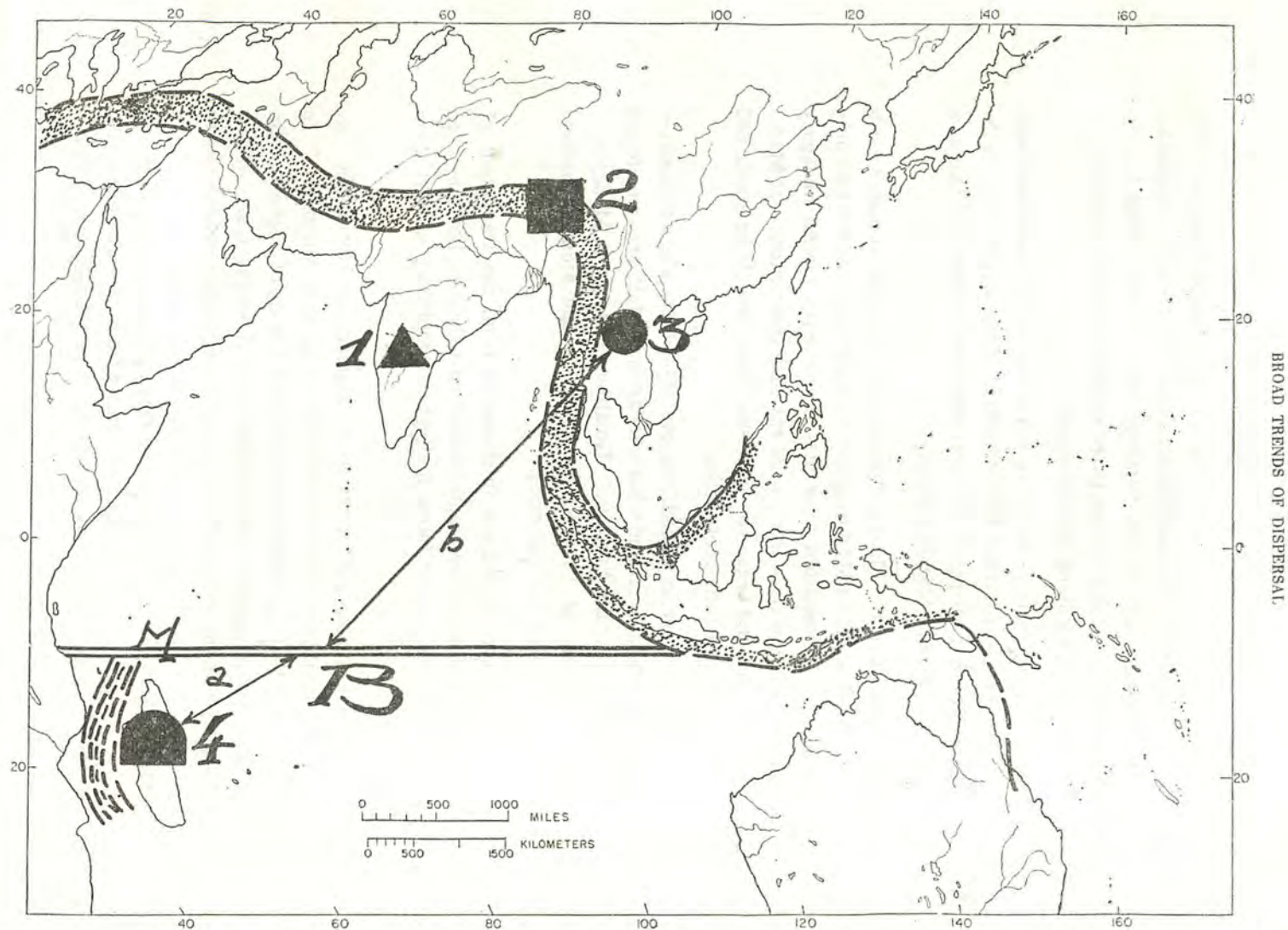
In map 8., marked with axes like those in map 2., I have added outlines of the areas holding birds with characters giving the claim to the controversial generic names: *Ipophilus*, *Leiopicus*, *Hypopicus*, *Picoides* and *Jungipicus* (= *Yungipicus*). These areas will be readily seen to lie along the west to east axis north of the Indian Ocean. These generalised piciforms, in the background of the modern genera, mirrored by *Campethera*, *Chloronerypes* and *Chrysoptilus* in the "tracks" westward from Africa to the New World, are called "generalized" by reason of the lack of accord over their affinities.

That they are "generalized" today argues that the ancestral stock from which these groups sprang were even more so. The tendency today is towards the convenient retention of *Dendropicos* and *Dendrocopos* alone but there is manifestly more to the taxogeny of these woodpeckers than such a classification suggests.

This presents us yet again with evidence that the front Senegal—Arabia—India—Malaysia etc. received ancestral stocks of taxa extant today and received them from lands generally to the south of the front—including lands which lay east of where Africa lies today.

Map 9. shows the main Jurassic geosynclines (stippled): the zones of sinking and upheaval—of active geographic and topographic change—in existence at the time when the radiation of "modern" life began. The synclines were in action until the Tertiary saw the rise of the Himalayas, the Alps etc. From the evidence available I should like to draw the following conclusions:

1. *a geosyncline promotes form-making in stock competent to evolve further, it promotes extinction, though sometimes with relictual survival, in stock not competent to evolve further.* The direct causes are the increased opportunities created for ecological adaptation, for segregation or for hybridization. For this reason the major tracks of "modern" life run in rather close agreement with the geosynclinal belts active in the late Mesozoic and Early Tertiary (see Croizat 1958: 2 b. p. 1611 et seq., Croizat 1962 p. 52. fig. 14 and p. 63. fig. 16):



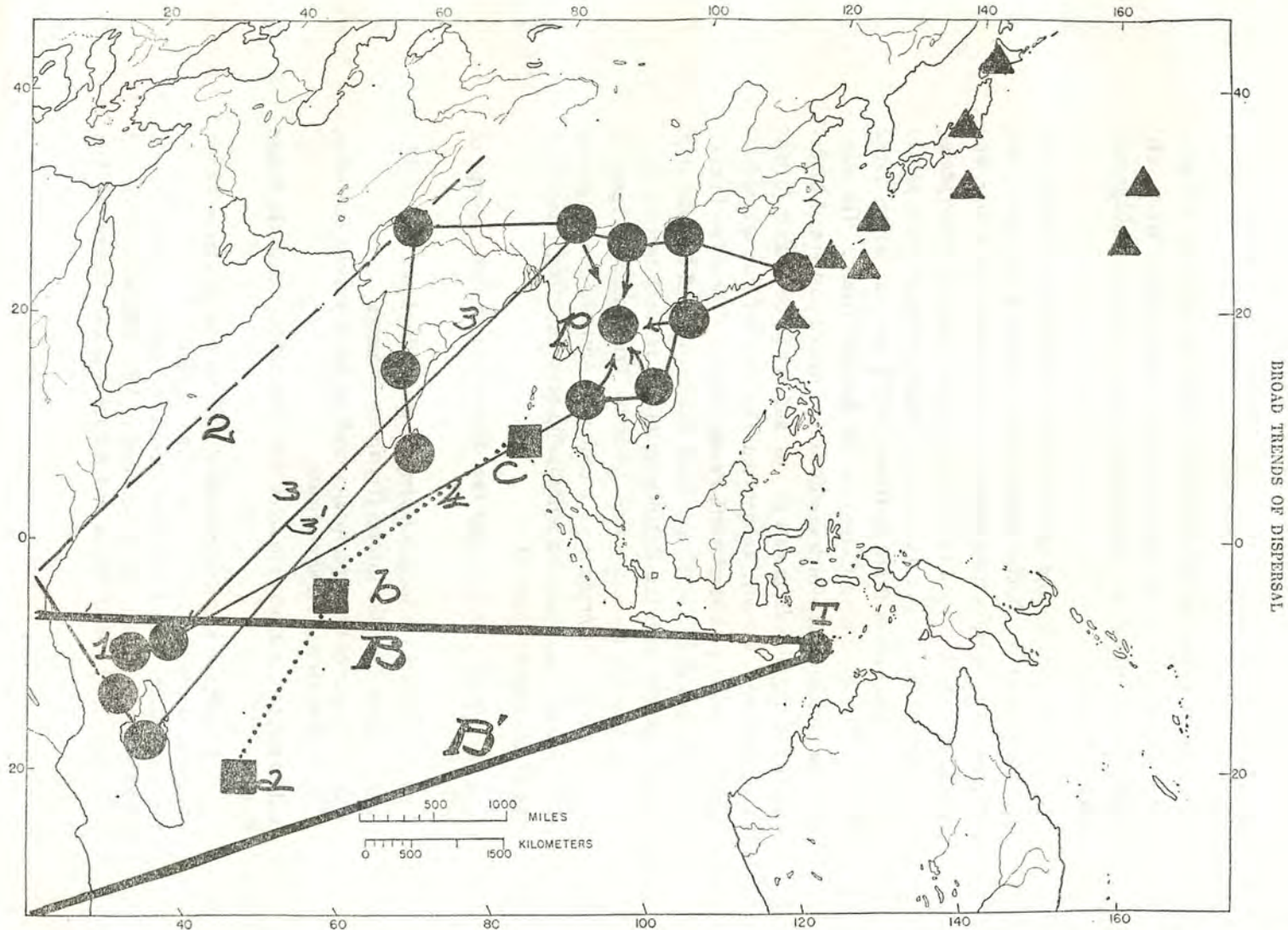
Map 9. To show the main Jurassic geosynclines (stipped areas; after Woodford 1965). See text p. 306.

The map shows, marked by a black triangle and the number 1, the relictual survival of ancient herpetofauna (Uropeltidae or Aniliidae: Uropeltinae *auct.* in the "Deccan plate". The solid square, marked 2, is to call attention to the example given by *Rhododendron* in form-making along the Himalayas.

2. Such life as evolved in the region along axis b. had links with Africa, yet has survived into "modern" times largely only in the cases where its dispersal was northward and eastward. This as a direct result of geological history.
3. The opening of the Mozambique channel (marked on map 9. with broken lines and an M) during mid-Jurassic times—after which only temporary connections were present, since the typical Malagasy plants and animals scarcely used any such connections—set Madagascar apart and began the break-up of the land lying south and west of the Jurassic geosyncline.
4. At an early stage in passeriform evolution there was a connection between Madagascar and what is today Indo-Malaysia—manifested for example by the "archaic" Timaliinae endemic to Madagascar and the mass of "modern" babblers in and around Thailand (symbols 4 and 3 on the map).

These conclusions are fundamental from the standpoint of chronology and whilst seemingly far-fetched in their implications when propounded in 1952 the latest findings in geophysics support them admirably.

There are no piciformes in Madagascar or Australasia. By contrast *Chrysococcyx* is not in Madagascar but is in Australasia. In discussing the latter **Friedmann**—once again talking of a spread from southern Asia—suggests a route to the north of Madagascar. Whilst I disagree with his suggested timing for the separation of Madagascar and with the direction of his spread, the principle of a "northern route" is appropriate. This can be seen again in these small woodpeckers where a "track" (B) can be drawn from central Tanganyika to Timor—a line which runs clearly north of Madagascar. We can



Map 10. To show different "tracks" across the Indian Ocean. For explanation see text p. 308. Thailand, marked with a solid circle at 'p' occupies an interesting position.

also connect *Promerops* in South Africa with the rest of the Meliphagidae to the east of the central Lesser Sundas with a "track" (B) from South Africa to Timor—this time south of Madagascar. (See map 10.).

Let us plot on the same map the seasonal movement of the migratory races of *Cuculus poliocephalus*. Peters (1940) gives two resident races: *lepidus* from Malaya to the Sundas and Timor, and *insulindae* in Borneo; and two migrants: one, nominate *poliocephalus*, breeds in the Himalayan region east to Japan and migrates in part to Africa. Mackworth-Praed & Grant (1957) give the winter range there as "Lamu, Kenya Colony to the Zambesi river". The other migrant race is *rochii* which breeds in the forested portions of Madagascar and migrates from east to west and in part on to East Africa: "Uganda, Kenya Colony, Tanganyika Territory and Portuguese East Africa" according to Mackworth-Praed & Grant. These two lines of migration are shown by broken lines numbered 2 and 1 on the map. Taken together with the distribution of the resident species, this I believe supports the contention made by Friedmann, in regard to certain species of *Chrysococcyx* breeding in Australia and migrating to the Sundas, that there is a relationship between seasonal migration and biogeographic dispersal.

Let us add to the map the distribution of three groups of bulbuls:

- as solid circles the species *Hypsipetes madagascariensis*
- as solid triangles the species *Hypsipetes amaurotis*
- as solid squares the superspecies made up by *Hypsipetes borbonicus*, *H. crassirostris* and *H. nicobariensis*.

and connect them up so as to show their connections across the Indian Ocean.

I could add many other examples to this map but I have, I hope, made the point that at the time of the dispersal of the ancestors of these and other taxa the Indian Ocean was quite different—indeed much of it was land (see reproduction of Van Bemmelen's "Geotectonic Map of the East Indies and Adjacent Areas" in Croizat 1968, p. 152).

Hence the "tracks" that I have drawn—both in this map and others—often knife across the oceans of today as though they were land. We cannot today reconstruct the "Indian Ocean" as it was in every detail in the Jurassic/Early Cretaceous but the distribution patterns of today, collected and listed in many volumes, are by-products of such geography and its change over the years.

The distribution pattern of *Hypsipetes madagascariensis* is but one clue for the competent biogeographer, to the importance of Madagascar (cf. *Bernieria*: Pycnonotidae and *Neomixis*: Timaliidae), which was evidently a centre of evolution of babblers and bulbuls.

I remarked above that there are no woodpeckers in Madagascar. Returning to that now I suggest that this absence implies that their ancestral stocks in dispersing followed "tracks" that did not touch there. They are also absent from Australia—although some have "crossed Wallace's line" to Alor and the Celebes—for the same reason.

By contrast one cannot categorically use this reason for *Chrysococcyx* because the problem is at a different level (or time); the *Cuculidae* are by no means absent from Madagascar—they are represented by the entire sub-family Couinae plus *Cuculus*, *Centropus* and *Pachycoccyx*. *Chrysococcyx* may once have existed in Madagascar and it may since have become extinct there. Consideration of *Chrysococcyx sensu stricto*, which is limited to Africa, against the ranges of the other 4 genera of cuckoos, accepted by Peters, which are restricted to Africa, suggests a recurring and typical pattern of west and east distribution which argues against extinction or previous existence of Madagascar stock.

Early in this note I mentioned "origins" for species of *Dendrocopos* occurring in Thailand. The genus numbers some 33 species and 210 races of which 6 species (17%) and 10 races (4.8%) occur in Thailand—note the disparity between 'species: race' ratio in Thailand against total figures.

The species *Dendrocopos major* leads the genus with, according to Peters, 27 races. If we cut Eurasia in two along a line from the eastern end of the Taimyr peninsula in the north to Cape Comorin

(tip of India) in the south the races accepted by Peters lie: 18 to the west, 9 to the east. Peters includes a "*cabanisi* group" ranging from Manchuria southwards. Dement'ev & Gladkov (1951) exclude this group and accept 15 races to the west and 3 to the east.

Now conventional "zoogeography" would arrange these facts as follows:

1. Most forms are western.
2. Therefore the origin of the group is western.
3. Therefore the present dispersal is to be explained through a spread from west to east.

But then:

- a. How does one explain the *cabanisi* group?
- b. Why are these races distributed in a typically eastern fashion, with *stresemanni* restricted to Cachar, Manipur and Assam?
- c. In the Khasia hills *stresemanni* is sympatric with pitcher plants (*Nepenthes*), which occur too in the lowlands of New Caledonia and the highlands of New Guinea, and which would certainly seem to have dispersed into the Khasias from the south.

Biogeography examines the problem a little differently. Looking at the genus as a whole we note that the western element comprises: the bulk of *D. major*, *D. leucopterus*, *D. syriacus*, and *D. medius*. The eastern element—within the Old World—comprises: *D. atratus*, *D. macei*, *D. canicapillus*, *D. kizuki*, *D. moluccensis* and *D. maculatus*. Next the species centred on India need analysis as to their affinities, these species are *D. assimilis*, *D. himalayensis*, *D. darjellensis*, *D. auriceps*, *D. mahrattensis* and *D. hyperythrus*.

The resulting balance between east and west is probably no longer evidence for a purely western origin and this is further discredited by the distinctness of *mahrattensis* and of *hyperythrus*—the former almost assigned by Voous to *Leiopicus*, the latter assigned by Ripley (1961) to *Hypopicus*. The evidence points to the Indian species having origins out of a point immediately south of there—as Voous says "gondwanic"; and that *Dendrocopos* as seen today is attuned to the basic axes a. b. and c. in map 2. above.

This would tend to support the *eastern* affinities of the *cabanisi* group. The award of specific recognition to *D. cabanisi* advocated by the Russians is in taxonomic systematics dependant upon attainment of a level of differentiation. Happily the bird itself is not aware of the fuss or the rules. Formal lumping and splitting for systematic lists is just not flexible enough to handle a case like this (cf. also *Parus major*, *P. minor*, *P. bokharensis*—map 7. above).

Finally let me touch on the New World element. Here *Dendrocopos* has 10 species and 57 races, from Alaska to Patagonia with a huge gap from Central America to the vicinity of Bolivia. This gap is typical of much plant and animal life and is related to geotectonic alterations in the eastern coastline of the New World (Croizat 1962). Indeed the chronology of this evidences the length of time *Dendrocopos* has been in the New World. So too does the existence of "ladderbacks" on both shores of the Pacific. For a parallel case examine the Jays (*Garrulus leuceolatus*, *Lalocitta lidthii*—cf. Shuskin 1927—and the "American Jays").

F. NOTES ON *ZOSTEROPS*: PARTICULARLY IN AFRICA.

Mayr in Peters (1967) says of the Indo-Australian Zosteropidae "the relations . . . with those of Africa are obscure" (op. cit. p. 289 footnote). Moreau in the same work says of the African white-eyes "the very tentative and complicated taxonomy of the genus *Zosterops* in Africa must be stressed" (op. cit. p. 327 footnote).

The comments that follow are those of a biogeographer and I do not claim the qualifications to speak as an ornithologist.

In Croizat (1958) I dealt with *Zosterops* in Indo-Malaysia in Vol. 2b pp. 416-422. In my footnote on p. 417 I suggested the probability of two main aggregates, one involving *palpebrosa*, the other *japonica*. The present listing in Peters is not greatly different from my expectations. My suggestion was of course based upon the logical development of premises supported by "pan-biogeographical" analysis and synthesis,

The geographic link between African and Asian white-eyes is easily seen; indeed it is a standard one involving the islands off East Africa: Madagascar, the Comoros, the Mascarenes, Pemba and the Seychelles, where occur: *Z. maderaspatana*, *Z. mayottensis*, *Z. modesta*, *Z. mouroniensis*, *Z. borbonica*, *Z. olivacea* and *Z. vaghani*. A neat insular aggregate paralleled by *Dicrurus fuscipennis*, *D. aldabranus*, *D. fortificatus* and *D. waldeni* (Vaurie 1949). Such a massing normally heralds contacts with the Indo-Malaysian region as I have repeatedly shown.

Ripley (1961) synonymises the white-eye of the Laccadives: previously named *egregia*: with the nominate form of *Zosterops palpebrosa*. Nominative *palpebrosa* thus has a massive range in India almost matching the "gondwanic" *Dendrocopos mahrattensis*. The Laccadive population is nonetheless a geographic, though not necessarily phylogenetic, link to the African elements reaching the Seychelles.

The species *Z. ficedulina* (from Príncipe and Sao Tomé) and *Z. griseoventris* (from Annobon) provide a counterpart in the Gulf of Guinea. The importance of the islands here has been stressed earlier in these notes.

Four African species remain:

<i>Z. senegalensis</i>	21 races
<i>Z. abyssinica</i>	6 races
<i>Z. virens</i>	3 races
<i>Z. pallida</i>	monotypic

With the species *Z. senegalensis* as understood by Moreau in Peters are the following races of western distribution: *demeryi*, *stenocricota*, *kasaica*, *heinrichi*, and *quanzae*. These races form a group with a very consistent range.

The picture in East Africa is interesting for the races of *senegalensis* of Moreau are grouped by Mackworth-Praed and Grant (1957) as follows:

— <i>senegalensis</i>	}	under <i>Z. senegalensis</i>
— <i>anderssoni</i>		
— <i>eurycricota</i>		is given specific status

— <i>kikuyuensis</i>	}	under <i>Z. kikuyuensis</i>
— <i>mbuluensis</i>		
— <i>silvana</i>		is given specific status
— <i>jacksoni</i>	}	are "transferred" to <i>Z. virens</i>
— <i>kaffensis</i>		
— <i>stierlingi</i>		
— <i>stuhlmanni</i>		
— <i>kulalensis</i>	}	are "transferred" to <i>Z. pallida</i>
— <i>poliogastra</i>		
— <i>winifredae</i>		

By contrast Mackworth-Praed & Grant treat *flavilateralis* and *jubaensis* as races of *Z. senegalensis* whilst Moreau places them in *Z. abyssinica*. Moreau also recognizes 2 additional east african forms of *senegalensis* namely *reichenowi* and *toroensis*. Despite this there is general agreement on racial limits.

The assignment of races to species is however sharply different; let me then repeat once more that the working unit for the biogeographer must needs be the subspecies.

The races admitted by Moreau for *Z. virens* have a classical southern South African range, but the 4 races added to them by Mackworth-Praed and Grant would create an equally classical pattern of distribution running from the Cape through East Africa to Ethiopia—a pattern to be seen in plants, e.g. *Euryops* (Nordenstam 1968), or other birds e.g. *Pogonocichla* (Moreau 1951).

Unfortunately Mackworth-Praed and Grant do not stop here—a footnote adds that other races of *virens* occur in Fernando Po, the Cameroons, French Equatorial Africa and N. Angola south to South Africa. One can but assume from this footnote that the entire western group of *senegalensis* forms, *sensu* Moreau, is transferred to *virens*. This it seems to me is a more radical move.

Whether Moreau or Mackworth-Praed and Grant be right I find it hard to accept Mayr's comment in Peters that "to try to consolidate the two listings (of African and Indo-Australasian white-eyes) is not feasible at present". There is nothing intrinsic in the distribution of these birds that leads to such a conclusion.

G. IN CONCLUSION:

Although Herbert **Deignan** believed in the methods of enquiry that I have employed I anticipate that some readers will still feel that my views are untested, speculative and bold. In the case of such readers I hope that I have whetted their appetite and that they may tackle some of the 8000 pages of my earlier writings to find the substantiation that they seek.

Some, at least, of the conclusions that I reach are not new. They have been advanced before and I put them forward now changed only by the uniform method of enquiry that has been applied and which supports them.

Chapin (1932) commented that Madagascar had a poor representation of Ploceidae and Estrildidae. He wondered why the Ploceinae, old enough to be common to Madagascar and continental Africa, did not extend to Indo-Malaya in greater variety. His hypothesis was that "an early localization of the sub-family in southern Africa" seemed the most logical explanation. **Chapin** also considered it possible that many of the forest birds of Africa had been affected by "past intercourse with Asia". The direction of **Chapin's** thoughts is clear.

Many may consider my explanation of the occurrence of the controversial bullfinch *Pyrrhula murina* to be far-fetched. It is not however an isolated case. Directly parallel to it is the case of *Erithacus rubecula* which has a strikingly distinct race—*superbus*—in the highlands of Grand Canary and Tenerife, yet is otherwise represented in the islands by the nominate race (**Lack** 1946).

Conclusions which are to remain valid must be applicable broadly. It is easy for a naturalist who specialises in a small group to hypothesize in a vacuum and to write the "zoogeography" of that group if inexplicable factors can be put down to chance. Were he to look further his insoluble problems would be paralleled and the invocation of chance would be shown to be a lack of reasoning. Such naturalists repeat the behaviour of the astronomers before **Copernicus** who invented a new "epicycle" for what they could not otherwise explain.

The naturalist who faces a whole fauna or flora can no longer invoke the opiate "chance". **Deignan**, for example, was fascinated by the profusion of babblers in Thailand and he readily understood that the zoogeography of one must be consonant with that of each of the others. **Deignan's** interest in precise biogeography was certainly aroused in part by his early field experience of the Khun Tan range in northern Thailand. His first book (1945) commented extensively on the phenomenon of this "divide". Later he was struck by the importance of Prachuap Khiri Khan and its similarity to the Tenasserim limit mentioned by me (**Croizat** 1958). His untimely death has no doubt deprived us of some important thoughts on the biogeography of the Thai region.

In summary then I should like to emphasize the following points:

1. Biogeography is not subordinate to taxonomy, it is a distinct and fundamental biological science—a speciality that should be mastered in the same way as any other.
2. Biogeography is precise for it has at its core a method of analysis—both statistical and comparative—which is applied to the factual and known data of geographical distribution.
3. Such analysis, conducted on a sufficient scale to allow statistical averages, must needs yield positive results.
4. Anyone with an open mind who compares the patterns of distribution shown by plants and by animals over space and through time will be struck by the degree of repetition. Since the same palaeogeography has affected each taxa this should come as no surprise.
5. Whatever may be the absolute age of plants and animals the fossil record shows a definite spurt of "modernization" following the Permo-Carboniferous Ice Ages and a similar spurt after marked glaciation at the close of the Cambrian. It seems probable that prolonged severe glaciations wiped out "climactic" flora and fauna—which would have lacked ability to adapt—but stimulated the evolution of plants and animals with the potential to adapt: the "plastic" taxa.

6. It is statistically demonstrable that the threads of modern life point to the southern hemisphere. There are some exceptions, such as certain groups of coniferous plants. It was the southern hemisphere which suffered most under the Permo-Carboniferous glaciations, and this stimulus no doubt explains the massive spread over space and time of taxa whose primaeval ancestors were located there.
7. We do not know how life dispersed before the mid-Jurassic, but at about that time the Mozambique channel opened up and the break up of the existing landmasses commenced with a consequent establishment of centres of massing and development of "modern" life. Such development followed fundamental "tracks" according to the geographic possibilities of the time and the options available at any given time were constant factors affecting the dispersal of different taxa in like fashion. Despite subsequent changes in geography the patterns of dispersal then followed explain the patterns of distribution found today.
8. It is of course obvious that the evolution of the geography of the earth and of the life on earth proceeded together.
9. Geophysical data available today can be used to support the chronology of major tectonic events and thus the timing of dispersal.
10. "Tracks" that are seemingly "trans-oceanic" must be considered in the light of the geography of the time of dispersal and vice versa in that the geological events can be more easily fixed in time and an examination of their nature shows the potential of the "tracks".
11. It is not claimed that all modern taxa are of Jurassic age but rather that generalised ancestors of that age were then stimulated to evolve.
12. It seems safe to say that rapid evolution was taking place soon after the mid-Cretaceous amongst stock not unlike the avian taxa of today. This is supported by Howard (1950) in his examination

of the fossil record, particularly if one bears in mind that the age of fossilization is certainly preceded by the age of origin.

13. Distribution or dispersal is capable of analysis by methods of statistical probability and each hypothesis of "chance dispersal" or of a "centre of origin" should be submitted to a searching analysis using a broadly based sample.
14. The analyses made in this paper do not conflict with any of the *facts* in the cases examined nor do the overall conclusions. They may *indeed* conflict with hypothetical views that have been advanced.
15. Whilst the major centres of massing and evolution of plants and animals were established no later than the early Cretaceous, it is not claimed the their limits have been constant. Indeed it is clear that climatic and geological events have been a secondary influence.
16. Taxogeny is an indispensable adjunct to taxonomy and their differences have been explained above.
17. Thailand is an exceedingly interesting biogeographic location. The untimely death of Deignan has rendered examination of its biogeography a sad blow and I hope this article will bring the possibilities to the attention of other, younger naturalists.

LIST OF REFERENCES

- AMADON, D. 1944 The Genera of Corvidae and their relationships.
Amer. Mus. Novit. No. 1251.
- AMADON, D. 1965 Position of the Genus *Neospiza* Salvadori.
IBIS **107** : 395-396.
- BAKER, R.H. 1951 The Avifauna of Micronesia, its Origin, Evolution and
Distribution.
Univ. Kansas Publs. **3**(1) : 1-359.
- BANNERMAN, D.A. 1953 The Birds of West and Equatorial Africa, I. (Struthi-
onidae to Picidae), II (Eurylamidae to Ploceidae).
Edinburgh & London (Oliver & Boyd).
- BLAKE, E.R. 1953 Birds of Mexico.
Univ. Chicago Press.
- BLAKE, E.R. & VAURIE, C. 1962 Family Corvidae. In Peters's Checklist of Birds of the
World. Vol. XV. Edited by E. Mayr & J.C. Greenway.
Mus. of Comparative Zoology, Cambridge, Mass.
- CAIN, S.A. 1943 Criteria for the indication of center of origin in plant
geographical studies.
Torreya **43** : 132 et seq.
- CAVE, F.O. & MACDONALD, J.D. 1955 Birds of the Sudan.
Edinburgh & London (Oliver & Boyd).
- CHAPIN, J.P. 1932 The Birds of the Belgian Congo, Pt. I.
Bull. Amer. Mus. Nat. Hist. **65** : 379.
- CHASEN, F.N. 1935 A Handlist of Malaysian Birds.
Bull. Raffles Mus., Singapore No **11** : 1-389.
- CROIZAT, L. 1952 Manual of Phytogeography. The Hague.
- CROIZAT, L. 1958 Panbiogeography. Vols. 1, 2a, 2b. Caracas.
- CROIZAT, L. 1960 Principia Botanica, Vols. 1a, 1b. Caracas.
- CROIZAT, L. 1962 Space, Time, Form : The Biological Synthesis. Caracas.
- CROIZAT, L. 1967 An ecological problem with long roots : the growth
forms of *Eucalyptus*.
In : Trop. Ecol. (Varanasi, India) : 30.

- CROIZAT, L. 1967a. An Introduction to the subgeneric classification of *Euphorbia* L., with stress on the South African and Malagasy species. II.
In: *Webbia* **22**: 83.
- CROIZAT, L. 1968. The Biogeography of the Tropical Lands and Islands east of Suez-Madagascar: with particular reference to the dispersal and form-making of *Ficus* L. and different other vegetal and animal groups.
In: *Atti Ist. Bot. Lab. Crittog. Univ. Pavia*, ser. 6, **4**: 1-400.
- CROIZAT, L. 1968a. Introduction Raisonnée à la Biogéographie de l'Afrique.
In: *Mem. Soc. Broteriana* (Coimbra, Portugal) **20**: 1-451.
- CROIZAT, L. 1968b. The Biogeography of India: a note on some of its fundamentals.
In: *Proc. Symposium Recent Advances in Trop. Ecology* (Varanasi, India), Pt. II: 544.
- CROIZAT, L. (in prep.) Osservazioni sulla fitogeografia, ecologia e tassogenetica del genere *Rhododendron* L.
To be published in: *Atti Ist. Bot. Lab. Crittog. Univ. Pavia*.
- DEIGNAN, H.G. 1945. The Birds of Northern Thailand.
Bull. 186, Smiths. Inst., U.S. Natl. Mus.
- DEIGNAN, H.G. 1950. The races of the Collared Scops Owl, *Otus bakkamoena* Pennant.
In: *The Auk* **67**: 189.
- DEIGNAN, H.G. 1963. Checklist of the Birds of Thailand.
Bull. 226, Smiths. Inst., U.S. Natl. Mus.
- DEIGNAN, H.G. 1963a. Birds in the Tropical Pacific.
In: *Pacific Basin Biogeography* (Tenth Pacific Sc. Congress, Honolulu, Hawaii. 1961), Honolulu.
- DELACOUR, J. 1941. On the species of *Otus scops*
In: *Zoologica* **26** (2): 133
- DELACOUR, J. & VAURIE, C. 1951. Les Mésanges Charbonnières (Révision de l'Espèce *Parus major*).
In: *L'Oiseau Rev. Fr. Ornithol.* **20**: 91,

- DEMENT'EV G.P. & GLADKOV N.A. 1951 Ptizy Sovetskavo Soyusa, Vol. 1. Moskva (Moscow).
- DOBZHANSKY, T. 1951 Genetics and the Origin of Species, 3rd ed. No. XI, Columbia Biol. Ser. New York (Columbia Univ. Press).
- DORST, J. 1947 Révision Systématique du genre *Corvus*. In: L'Oiseau Rev. Fr. Ornith. **17** (n.s. No. 1) : 44.
- DORST, J. 1962 Les Migrations des Oiseaux. Paris (Payot)
- FRIEDMANN, H. 1968 The Evolutionary History of the Avian Genus *Chrysococcyx*. Bull. 265, Smiths. Inst., U.S. Natl. Mus.
- HARLAND, W.B. & RUDWICK, M.J.S. 1964 The Infra-Cambrian Ice Age. In: Scientific American **211** (2) : 28.
- HEIRTZLER, J.R. 1968 Sea-floor spreading. In: Scientific American **219** (6) : 60.
- HOWARD, H. 1950 Fossil Evidence of Avian Evolution. In: Ibis **92** : 1.
- LACK, D. 1946 The taxonomy of the Robin, *Erithacus rubecula* (Linn.) In: Bull. Brit. Ornith. Cl. **66**:55.
- MACKWORTH-PRAED, C.W. & GRANT, C.H.B. 1957 African Handbook of Birds, Ser. I, Vol. 1. Birds of Eastern and Northeastern Africa, (2nd edition). London, N.Y., Toronto (Longmans, Green & Co.).
- MAYR, E. 1967 Family Zosteropidae : Indo-Australian Taxa. In: Peters' Check-list of Birds of the World. Vol. XII. Edited by R.A. Paynter. Mus. of Comp. Zoology, Cambridge, Mass.
- MEINERTZHAGEN, R. 1926 Introduction to a review of the genus *Corvus*. In: Novit. Zool. **33** : 57.
- MEINERTZHAGEN, R. 1928 Some biological problems connected with the Himalayas In: Ibis **12** (ser. 4) : 499.
- MEINERTZHAGEN, R. 1951 Some relationships between African, Oriental, and Palaearctic genera and species, with a review of the genus *Monticola*. In: Ibis **93** (3) : 443.
- MEINERTZHAGEN, R. 1954 Birds of Arabia. Edinburgh & London (Oliver & Boyd).

- MOGGI, G. & PISACCHI, A. 1967 *Adumbratio Florae Ethiopicae*. 14 : Hypericaceae
In : *Webbia* **22**:233.
- MOREAU, R.E. 1951 Geographical Variation and Plumage Sequence in *Pogonochila*.
In : *Ibis* **93** : 383.
- MOREAU, R.E. 1967 Family Zosteropidae : African and Indian Ocean Taxa.
In : Peters's Checklist of Birds of the World. Vol. XII.
Edited by R.A. Paynter, Mus. of Comp. Zool, Cambs, Mass.
- MOREAU, R.E. & CHAPIN, J.P. 1951 The African Emerald Cuckoo, *Chrysococcyx cupreus*.
In : *The Auk* : **68**:174.
- NORDENSTAM, B. 1968 The Genus *Euryops*, Part I : Taxonomy
In : *Opera Botanica* (Lund Univ.) No. 20.
- PAYNTER, R.A., Jr. 1968 Introduction to Peters's Checklist of Birds of the World.
World. Vol. XIV. Edited by R. A. Paynter, Jr., Mus. of
Comp. Zool., Cambridge, Mass.
- PETERS, J.L. 1940 Check-list of Birds of the World. Vol. IV.
Harvard Univ. Press., Cambridge, Mass.
- PETERS, J.L. 1948 Check-list of Birds of the World. Vol. VI.
Harvard Univ. Press., Cambs., Mass.
- PHELPS, W.H. & PHELPS, W.H. Jr. 1958 Lista de las Aves de Venezuela con su distribución
Tomo II, Pt. I : No Passeriformes.
In : *Bol. Soc. Venezolana Cienc. Nat.* **19**, No. 90:1-317.
- RAND, A.L. 1951 Birds from Liberia with a Discussion of Barriers
between Upper and Lower Guinea subspecies
In : *Fieldiana* (Zoology) **22**, No. 9: 558.
- RAND, A.L. 1968 Footnote 2, on p. 231 of Peters's Check-list of Birds of
the World. Vol. XIV. Edited by R.A. Paynter Jr.
Mus. of Comp. Zool., Cambridge, Mass.
- RAND, A.L. & TRAYLOR, M.A. Jr. 1953 The Systematic Position of the genera *Ramphocaenus*
and *Microbates*.
In : *The Auk* **70** : 334.
- RIPLEY, S.D. 1949 Avian relicts and double invasions in peninsular India
and Ceylon.
Evolution III: 150-159.
- RIPLEY, S.D. 1961 A Synopsis of the Birds of India and Pakistan. Bombay.

- SALOMONSEN, F. 1934 Revision of the Madagascar Timaliine Birds.
In: Ann. & Mag. N.H. **14** (ser. 10) : 60.
- SHUSKIN, P.P. 1927 On the affinities of *Lalocitta*.
In: Ibis **3** (ser. 12) 518.
- SMYTHIES, B.E. 1960 The Birds of Borneo.
Edinburgh & London (Oliver & Boyd).
- STRESEMANN, E. 1925 Beitrage zur Ornithologie der indo-australischen
Region. II. Kurze Ueberucht uber die indo-Malayischen
Zwergheulen.
Mitt. Zool. Mus. Berlin, **12** : 191-195.
- SWAN, L.W. 1961 The Ecology of the High Himalayas.
In: Scientific American **205** (4) : 68.
- VAN STEENIS, C.G.G.J. 1948-1954 Flora Malesina, Ser. I, Vol. 4.
Djakarta (Noordhoff-Kolff N.V.)
- VAURIE, C. 1949 A Revision of the Bird Family Dicruridae.
In: Bull. Amer. Mus. Nat. Hist. **93** (art. 4) : 199.
- VAURIE, C. 1950 Notes on some Asiatic Titmice.
In: Amer. Mus. Novit. No. 1459.
- VOOUS, H.K. 1947 On the History of the Distribution of the genus *Dendrocoptes*, I. (Thesis). Amsterdam.
- VOOUS, H.K. 1949 Distributional History of Eurasian Bullfinches
In: The Condor **51** : 52.
- WENDT, H. 1967 Auf Noahs Spuren Die Entdeckung der Tiere.
Hamm (Westfalen) Verlag. KG.
- WIEBES, J.T. 1968 Catalogue of the Coleoptera : Cetoniidae in the Leiden
Museum 1. *Goliathus* Lamarck, sensu lato.
In: Zoolog. Mededel. Rijksmus. Nat. Hist. Leiden,
Deel **43/3** : 19.
- WOODFORD, A.O. 1965 Historical Geology.
San Francisco & London (Freeman & Co.)